RESPONSES OF BIRD POPULATIONS TO HABITAT LOSS AND FRAGMENTATION: OCCUPANCY AND POPULATION DYNAMICS OF TROPICAL FOREST BIRDS IN COSTA RICA

A Dissertation

Presented to the Faculty of the Graduate School

of Cornell University

In Partial Fulfillment of the Requirements for the Degree of

Doctor of Philosophy

by

Viviana Ruiz-Gutierrez

August 2009

RESPONSES OF BIRD POPULATIONS TO HABITAT LOSS AND FRAGMENTATION: OCCUPANCY AND POPULATION DYNAMICS OF TROPICAL FOREST BIRDS IN COSTA RICA

Viviana Ruiz-Gutierrez, Ph.D.

Cornell University 2009

Current patterns of worldwide population declines and species extinction have been attributed to the destruction, fragmentation, and degradation of natural areas. Much research has thus far focused on estimating how populations respond to changes in the amount and configuration of available habitat. I addressed this question by testing for effects of habitat fragmentation on forest bird species in southwestern Costa Rica.

I tested for fragmentation effects on survival of adult individuals of the white-ruffed manakin (*Corapipo altera*), and found a significant difference in annual apparent survival rates for adults marked and recaptured in forest fragments vs. a larger forest reserve. Therefore, habitat loss and fragmentation is likely driving the dynamics of manakins by lowered population growth rates through reductions in survival. I used the same manakin population to test for population structuring and genetic diversity. Individuals from all fragments comprised a single genetic population, and that the fragments were likely at migration-drift equilibrium. I found only modest levels of differentiation, and did not detect a correlation between genetic diversity and fragment size.

If community-level effects using a dynamic, multi-species hierarchical model applied to observational data. I found higher levels of occupancy and colonization of forest across species in contrast to the non-forest matrix. Species' prior classification

of forest dependency was a poor predictor of overall occupancy dynamics of both habitat types.

I lastly tested for effects on habitat quality, and found an effect of reduced area on composition and abundance of forest interior tree species relative to pioneer species. There was also an effect on tree height in forest fragments relative to control sites, dependent on the canopy strata of the tree ($t = 5.20$, $p < 0.0001$). Therefore, deforestation could potentially reduce the quality of forest fragments for tropical bird communities through changes in food resources and availability of microhabitats, as observed by changes in the structure and composition of the tree community.

Estimating how tropical bird populations respond to deforestation, through effects on survival, dispersal, and occupancy dynamics, has furthered our understanding on how organisms in diverse communities respond to anthropogenic changes in the environment.

BIOGRAPHICAL SKETCH

Viviana Ruiz-Gutierrez was born in San Jose, Costa Rica, on August 14^{th}, 1978. She attended an elementary school for the arts, but would skip most of her classes to climb and play on every tree her limbs could reach. At the age of ten, she moved to Lexington, KY, when her mother, Sonia Gutierrez, received a Fulbright Scholarship to get her Master's degree. This place was *very* different from her home town of Heredia, and she had a hard time understanding things like why a breaded and fried hot dog on a stick was considered food. After two long years, her mother went on to pursue a Ph.D. in Amherst, MA. It was in this amazing college town that she stayed for Junior High and High School. She spent a large chunk of those eight years with her friends biking, canoeing and backpacking, until the time came to apply to college. Although she wanted to be a biologist, she had no real concept of what that meant, and missed home and her childhood days of mango-induced food comas.

Viviana then went back to Costa Rica, and spent almost two years volunteering and working in many different places banding birds, working for conservation projects, patrolling sea turtle beaches, guiding tours, teaching Spanish, and even bartending. She then attended the National University of Costa Rica to major in Tropical Biology. Four years and many hours of field work later, she moved to Ithaca, NY, for graduate school. Every year while at Cornell, she happily went to Costa Rica to do her dissertation research on birds at the Las Cruces Biological Station. Viviana hopes to do conservation science work in the tropics for many years to come, never straying too far from home. Eventually, she hopes to retire on a hill next to her birds at Las Cruces, enjoying sunsets over the deep blue ocean she loves so much.

I dedicate this dissertation to my courageous mother, Dr. Sonia Gutierrez Villalobos,

and my loving sister, Dr. Melisa Ruiz Gutierrez.

ACKNOWLEDGMENTS

I would like to thank my co-advisor Thomas Gavin, for being my mentor, colleague and friend, and for always reminding me of the value that lies in always knowing the natural history of your study system. I also owe much gratitude to my other co-advisor, Andre Dhondt, for he was both a critic and the greatest believer in my work. Andre also taught me the crucial process of transforming my passion for conservation into exciting ecological questions and testable hypotheses. I also want to thank my committee member Evan Cooch, for opening my eyes to the implications resulting from the fact that observations are not always representative of the biological state of a system.

I would like to thank Wesley Hochachka, for all of his patient advice and comments on everything from my first proposals to the introduction of this thesis. Also, I would like to thank Andrew Royle and Elise Zipkin at the USGS Patuxent Wildlife Research Center for the motivating and hopefully long-lasting collaborative work that made Chapter 2 possible. I also owe thanks to the Dhondt lab staff for all of their patience, comments and encouragement over the years: Dave Bonter, Caren Cooper, Daniel Fink, Meena Hannibal, and Stephan Hames, and Doug Morin. I want to thank other staff at the Lab of Ornithology: Karen Purcell, Ken Rosenberg, and specially Eduardo Inigo-Elias, for being a true mentor in how to channel a passion for tropical bird conservation into on the ground policy and change.

I would also like to thank all of the staff at the Las Cruces Biological Station: the kitchen staff Lidieth, Maritza, Flor, Mayra, Flor, as well as Rodolfo Quiros, Andrea, Ariadna Sanchez, Yorleny Vargas, and Zak Zahawi. I am also grateful for the friendship and help in the field from Guillermo Duran, Mauricio Paniagua, Allen Ilama, and Victor Milla. I want to thank Jacob Barnett and Javier Fernandez-Vega for trusting my project with their honors' thesis' and all of the hard work it entailed; Jim Zook, for helping me find my field sites my first year, and continuing to help collect data every year of the project; Daniel Souweine for bravely coming down to help mist-net birds for an entire field season. But none of my field work would have been possible without my field crew: Jeisson Figueroa, Michael Atencio, and Breiner Serrano; I would have never survived (literally at times) without you.

I truly enjoyed being in such a dynamic University, full of wonderful friends and interesting colleagues, whom I hope to not loose touch with over the years: Mike Booth, Nancy Chen, Marita Davidson, Jon DeCoste Sara DeLeon, Rebecca Dore, Josh Donlan, , Paul Hurtado, Mari Kimura, Paulo Llambias, Daniel Lebbin, Jen Moslemi, Dan Rabosky, Trevor Rivers, Martin Schlaepfer, Andy Schmidt Andrea Townsend, Arend Van Der Zande. I also had wonderful friends who kept me fed, sane, "hydrated", and laughing hysterically during the last legs of my degree: Mohammad Hammidian, Benjamin Hunt and Sarah States; and the now road crew of ladies armed with wine and spirits, laughter and facial masks: Kathryn Gardner and her G&S, Annie Rowe and her nunkies, and Cloelle Giddings with a Luna on her shoulders.

Lastly, I want to thank my family: my grandfather Juan Rafael Gutierrez Villalta (1900-1992) for inspiring us all to dream beyond the horizon; my stepfather Dr. Hideo Fujii, who brought me to Cornell the very first time; my mother, Dr. Sonia Gutierrez Villalobos, she is a caring and loving role model of what can be achieved with hard work and determination; my brother in-law Jason Kaden, for being a supportive and encouraging brother every step of the way of my crazy journey; and lastly, my sister, Dr. Melisa Ruiz Gutierrez, who has a heart that effortlessly warms a room, and who's hard work and dedication to improving the lives of her patients has been a constant source if inspiration in my life. Not a single day goes by that I am not grateful for all of the support, guidance, patience and love she has given me.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

CHAPTER 1

INTRODUCTION

Current patterns of worldwide population declines and species extinction have been strongly linked to the destruction, fragmentation, and degradation of natural areas through the expansion of agriculture and urbanization (Sala et al., 2000). Recent decades have been witness to an insurgence of research focused on estimating how changes in the amount and configuration of available habitat affect how animal populations occupy, reproduce and survive across habitat types in a landscape (Franklin et al., 2002). This body of work has built a broad base of knowledge with regards to how animal populations respond to factors related to the process of habitat loss and fragmentation, like reduced area and isolation, and extensive reviews can be found elsewhere (Andren, 1994; Ewers and Didham, 2006).

At the onset, research on fragmentation effects on animal communities and populations focused on estimating changes in patterns of distribution across habitat types in human-modified landscapes, assuming that individuals distribute themselves as to maximize their level of fitness (*i.e.* maximize reproductive success). When faced with contrasts in habitat quality, mobile organisms are highly likely to distribute themselves as to reflect tolerance or aversion to habitats perceived as having "lower" quality, or habitats that pose fitness cost. Therefore, observed differences in patterns of species occurrence provided insight into the likelihood of populations to adapt and persist in fragmented landscapes. Information solely on changes in distributions limits the applicability of predictions on the likelihood of extinction of species and populations in the face of habitat loss and fragmentation. The need to predict the long-term persistence of populations, coupled with advancements in relevant statistical tools, prompted the transition of research from community-level effects, to a focus on demographic responses of populations.

A large proportion of research dealt with fragmentation effects on dispersal, survival, and reproductive success of populations. The bulk of the work was done on avian populations, where, for example, proximity to habitat edges has been strongly linked to an increase in nest predation, causing reductions in reproductive success for song bird species nesting near edges of forest fragments (i. e. Donovan et al., 1997). There are fewer examples on the effects of habitat fragmentation on survival (Lampila et al., 2005), but there is evidence suggesting that adult birds residing in forest fragments do not live as long as adults of the same species residing in more continuous forests (Bayne and Hobson, 2002; Doherty and Grubb, 2002). This and other relevant work provided a much needed knowledge base on fragmentation effects on populations.

Despite advances, we are still far from being able to predict the mechanisms by which fragmentation is affecting demographic processes of populations, as well as the key drivers behind these changes. One of the main limitations to our understanding of how populations respond to habitat loss and fragmentation is the geographical bias of our knowledge. Most research to date focusing on estimating demographic responses of populations has taken place in temperate regions (Lampila et al., 2005). Tropical ecosystems harbor the highest proportion of threatened species that are highly likely to vary from temperate species with regards to what demographic variables are most affected by habitat loss and fragmentation.

To a lesser extent, our ability to predict likelihood of extinction is limited by the fact that the estimation of demographic responses of populations and related processes was, until recently, largely confounded by failures to correct for the fact that observations of ecological systems are composed of both a biological component, and the filters imposed by the process of collecting these data (Nichols, 1992; Williams et al., 2002). Recent developments in statistical tools have vastly improved the accuracy of our inferences, as well as increased the feasibility of these estimations. These relevant tools have provided an accessible framework with which to model changes in demographic parameters as a function of biotic (*i.e.* competition) and abiotic (*i.e.* patch size) factors as related to habitat loss and fragmentation.

I address these limitations in this thesis by estimating changes in how species occupy and survive in a fragmented landscape. I focused on community and population-level responses to human-induced changes in landscape structure in a highly understudied tropical system, applying novel and relevant statistical tools. More specifically, I focused on the responses of tropical bird populations to loss and fragmentation of mid-elevation forests of southwestern Costa Rica.

The second Chapter begins by testing for fragmentation effects on survival of adult individuals of the white-ruffed manakin (*Corapipo altera*) in southern Costa Rica. How forest fragmentation affects avian survival had only been shown in two previous studies in temperate systems prior to this study, but had never been shown across multiple sites and years in tropical systems (Bayne and Hobson, 2002; Doherty and Grubb, 2002). Survival and recapture rates were estimated using mark-recapture analyses based on capture histories from forest patches and four sites in a larger forest reserve. I found a significant difference in annual adult local survival rates for individuals marked and recaptured in forest fragments vs. individuals marked and recaptured in a larger forest reserve (χ^2 = 5.0220; df =1; P= 0.025), but did not find any differences in capture probabilities (χ^2 = 0.022; df =1; P= 0.645). Therefore, habitat loss and fragmentation is likely driving the dynamics of white-ruffed manakins, and other long-lived tropical species, by lowering population growth rates through reductions in adult survival. These observed effects on adult survival do not mean that they affect other population-level processes, like successful dispersal of young. Habitat fragmentation might be reducing the survival of adult individuals through increased mortality during movement between patches, or through a reduction in the quality of the resources on which they depend.

I, therefore, explored patterns of population structuring and genetic diversity in populations of the same species, the white-ruffed manakin, presented in Chapter 3. These results suggest that manakins may retain substantial connectivity via inter-fragment dispersal, despite habitat fragmentation effects on survival of adult individuals. We sampled 159 manakins, and genotyped these birds at 13 highly variable microsatellite loci. I focused on adult individuals during the breeding season from forest fragments and two larger control sites. Bayesian clustering methods revealed that birds from all fragments comprised a single genetic population, and that the fragments were likely to be at migration-drift equilibrium. This population showed only modest levels of differentiation, and we found no correlation between genetic diversity and fragment size.

In these initial studies, I had focused on how the population of one species in our study region responded to the effects of habitat loss and fragmentation, showing increased but delayed extinction probabilities for white-ruffed manakins residing in forest fragments. However, if there is a fitness cost associated with non-forest habitats in this system, as I observed by reductions in survival in forest fragments, we should detect patterns of spatially-explicit habitat use between forest and non-forest habitat types, given that this bird community is largely forest-adapted.

I address this question in Chapter 4, as well as the more general question of who in the community is most likely to respond adversely to changes in the amount and configuration of available habitat. I broadly quantified potential effects of the inter-patch matrix habitats surrounding forest remnants by estimating occupancy and colonization of forest and the surrounding non-forest matrix. I used a multi-year, multi-species, multi-level model applied to observations of species that make up the diverse bird community of southwestern Costa Rica. I found higher levels of occupancy and colonization of forest across species in comparison to the non-forest matrix. Species' prior ecological classification of forest dependency was a poor predictor of overall occupancy dynamics of both habitat types. Based on my analyses, I was able to create a rigorous assessment of the 39 species of greatest conservation concern, defined by having high estimates of continued occupancy of forest, and low estimates of continued occupancy and colonization of non-forest, and thus they were the most likely to affected negatively by habitat loss and fragmentation in this region.

So far, all of my analysis made the assumption that forest fragments are lower in quality than larger, more continuous tracts of forest. I address the validity of this assumption in Chapter 5 by testing for changes in habitat quality for the community of tropical birds in our study region of southwestern Costa Rica. I found a significant effect of reduced area on tree species composition and abundance of forest interior relative to pioneer species ($p < 0.0001$ for each). Therefore, forest fragmentation probably reduces habitat quality for this bird community through a reduction and change of tree mediated food sources. I also found a significant effect on height in forest fragments relative to control sites ($t=5.88$, $p = 0.0001$), and there was strong support for this effect to vary dependent on the canopy strata of the tree ($t= 5.20$, $p < 0.0001$). Therefore, forest fragmentation has additional significant impacts on the structural complexity of remnant fragments through reductions in height of canopy strata. These effects were not significantly affected by distance from the edge. The increased degree of overlap between canopy strata is likely to reduce or eliminate microhabitats associated with these strata, and reduce resources linked to foraging and breeding sites. Therefore, fragmentation of tropical forests could potentially reduce the quality of the habitat for tropical bird communities through changes in food resources and availability of microhabitats, as observed by changes in the structure and composition of the tree community. The ecological integrity of these fragments is likely to continue to deteriorate, and their long-term potential to serve as habitat for birds and other organisms is likely to decrease unless action is taken to mitigate these effects.

Conclusions and closing remarks

"To those familiar with the manifold of complexities…in real populations, our "basic" models may seem oversimplified to the point of lunacy"- Roy Anderson and Robert May, 1992.

Current patterns of worldwide population declines and species extinction driven by habitat loss and fragmentation have presented population ecologists with the challenge to define what biotic and abiotic factors are strong determinants of the likelihood of long-term persistence of populations. In other words, the pressing question is: who is most at risk in fragmented and degraded systems? This overarching question has been at the forefront of research in the fields of evolutionary, population, and conservation biology in the past few decades. I began to address this question in this dissertation using relevant statistical tools in an understudied tropical system. My research on the effects of fragmentation on survival, dispersal, and occupancy dynamics of a tropical bird community were done applying an approach clearly aimed at improving our capability to make demographic projections of what bird populations are likely to go extinct in the face of deforestation.

I found that individuals of the white-ruffed manakin that reside in forest fragments are not able to survive as long as individuals in larger forests, and therefore, not able to produce as many successful young. The genetic inference showed that despite these effects, individuals still appear to be dispersing through the landscape. What is a likely outcome for this species in the landscape? To fully address this question, we must go beyond demographic projections, and examine how changes in fitness-related life-history traits are likely to dynamically influence long-term persistence. Considering the high estimates of survival for this species, if population sizes of this forest bird do not decline past a critical level, reduced adult survival over the long-term could lead to an increase in reproductive effort and higher frequency of individuals with earlier reproductive onset in this population (Reznick et al., 1994; Reznick and Endler, 1982; Reznick et al., 1990). Does this hold true for the other numerous bird species in the community? Is apparent survival for adults for most species equally high and reduced by forest fragmentation? Or is there a high degree of variation in not just survival, but other fitness-related life-history traits, and thus responses to changes in mortality and reproductive success vary highly as well? For example, for species that appear to be faring better in fragmented systems, could a plausible explanation be that these individuals do not live as long, and are thus not as affected by increases in adult mortality?

Answering these questions is a critical step in linking life-history traits with the likelihood of extinction, and could improve our capability to predict what species and populations are most at risk of extinction. The key challenge to answering this question is one common to all research that contrasts demographic parameters of populations of individuals that inhabit different habitat types. If we recall, apparent survival is a product of true survival probability and how likely an individual is to remain in the sampling area, otherwise known as fidelity. This is because if an individual is not captured again, we can not differentiate in a live encounter, mark-recapture study if an absence means the individual is dead, or simply was no longer available for capture. Our estimates of survival are therefore strongly dependent on how likely individuals are to remain in the study area. Habitat types that differ in quality are likely to differ in not only fidelity, but also in their probability of capture if movement patterns differ between habitat types. Therefore, the only way to contrast differences in demographic rates of individuals is to use a robust design framework (Kendall et al., 1997), and test for not only differences in recapture probabilities among habitat types, but also if there are differences in movement-related parameters of temporary emigration. This is the best way to test if apparent contrasts between demographic rates are not just a function of differences in capture probabilities or movement patters. Another key factor that also influences fidelity is the spatial scale of inference used to estimate movement and survival parameters for each habitat type, specifically if individuals use more than one within and between seasons. Habitat-specific estimates for individuals with home-ranges that span across multiple habitat types will likely be biased as reflected by the proportion of time spent at each habitat type. Bias resulting from differences in spatial scale of inference for demographic parameters was shown for the long-lived, highly territorial spotted owl (*Strix occidentalis*), where estimates of survival increased with increasing area of inference (Zimmerman et al., 2007).

Moving away from individual species to community-level effects, I have shown that bird species in this community favor forest in comparison to non-forest habitats, and that forest fragmentation is impacting a much larger proportion of the community than previously thought. Bird species classified as open or degraded habitat species, and thus previously considered to not be negatively affected by forest fragmentation, were shown to occupy and colonize forest at much higher rates than previously thought. These results regarding occupancy and colonization would have been masked had I focused just on “habitat specialists” or “forest birds,” or failed to correct for the fact that detection of individuals is imperfect, and differs for each species and habitat type.

Still, I cannot make the claim that species are choosing forest over non-forest without further evidence associating a fitness cost with non-forest habitats. Our results make the assumption that patterns of occupancy dynamics (*i.e.* occupancy, colonization, extinction) are positively correlated with fitness-related life-history traits. This relationship might hold true for some species, but it could vary widely depending on the life-history traits themselves. The strength in correlation between indicators of abundance and fitness components has been shown empirically to vary depending on factors like territoriality and spatial aggregation of individuals (Aldridge and Boyce, 2007; Nielsen et al., 2005). Are there life-history traits we can identify for which occupancy is not a good indicator of habitat quality for individuals?

Estimating how tropical bird populations respond to deforestation, through effects on survival and differences in how species associate with habitats in the landscape, has furthered our understanding on how diverse communities of organisms are responding to changes in the environment. I have also provided further insight as to who might be most at risk, and begun to lay the groundwork of relating life-history traits with extinction risk. I plan to continue to carry out research in this exciting and challenging topic for many years to come, and hopefully impact along the way innovative conservation measures to mitigate human impacts on animal populations, and do my part in increasing the probability that lower latitudes remain diverse for many generations to come.

REFERENCES

Aldridge, C.L., and M.S. Boyce. 2007. Linking occurrence and fitness to persistence: Habitat-based approach for endangered Greater Sage-Grouse. *Ecological Applications*. 17:508-526.

Andren, H. 1994. Effects Of Habitat Fragmentation On Birds And Mammals In Landscapes With Different Proportions Of Suitable Habitat - A Review. *Oikos*. 71:355-366.

Bayne, E.M., and K.A. Hobson. 2002. Apparent survival of male ovenbirds in fragmented and forested boreal landscapes. *Ecology*. 83:1307-1316.

Doherty, P.F., and T.C. Grubb. 2002. Survivorship of permanent-resident birds in a fragmented forested landscape. *Ecology*. 83:844-857.

Donovan, T.M., P.W. Jones, E.M. Annand, and F.R. Thompson. 1997. Variation in local-scale edge effects: Mechanisms and landscape context. *Ecology*. 78:2064-2075.

Ewers, R.M., and R.K. Didham. 2006. Confounding factors in the detection of species responses to habitat fragmentation. *Biological Reviews*. 81:117-142.

Franklin, A.B., B.R. Noon, and L. George. 2002. What is habitat fragmentation? *Studies in Avian Biology*:20-29.

Kendall, W., J. Nichols, and J. Hines. 1997. Estimating temporary emigration using capture-recapture data with Pollock's robust design. *ECOLOGY*. 78:563-578.

Lampila, P., M. Monkkonen, and A. Desrochers. 2005. Demographic responses by birds to forest fragmentation. *Conservation Biology*. 19:1537-1546.

Nichols, J.D. 1992. Capture-Recapture Models. *Bioscience*. 42:94-102.

Nielsen, S.E., C.J. Johnson, D.C. Heard, and M.S. Boyce. 2005. Can models of presence-absence be used to scale abundance? - Two case studies considering extremes in life history. *Ecography*. 28:197-208.

Reznick, D., R.J. Baxter, and J. Endler. 1994. Long-Term Studies of Tropical Stream Fish Communities - the Use of Field Notes and Museum Collections to Reconstruct Communities of the Past. *American Zoologist*. 34:452-462.

Reznick, D., and J.A. Endler. 1982. The Impact of Predation on Life-History Evolution in Trinidadian Guppies (Poecilia-Reticulata). *Evolution*. 36:160-177.

Reznick, D.A., H. Bryga, and J.A. Endler. 1990. Experimentally Induced Life-History Evolution in a Natural-Population. *Nature*. 346:357-359.

Sala, O., F. Chapin, J. Armesto, E. Berlow, J. Bloomfield, R. Dirzo, E. Huber-Sanwald, L. Huenneke, R. Jackson, A. Kinzig, R. Leemans, D. Lodge, H. Mooney, M. Oesterheld, N. Poff, M. Sykes, B. Walker, M. Walker, and D. Wall. 2000. Biodiversity - Global biodiversity scenarios for the year 2100. *SCIENCE*. 287:1770-1774.

Williams, B.K., J.D. Nichols, and M.J. Conroy. 2002. Analysis and Management of Animal Populations: Modeling, Estimation, and Descision Making. Academic Press. 1040 pp.

Zimmerman, G.S., R.J. Gutierrez, and W.S. Lahaye. 2007. Finite study areas and vital rates: sampling effects on estimates of spotted owl survival and population trends. *Journal Of Applied Ecology*. 44:963-971.

.

CHAPTER 2

HABITAT FRAGMENTATION LOWERS SURVIVAL IN A TROPICAL FOREST BIRD

Abstract

Population ecology research has long been focused on linking environmental features with the relative fitness of populations. The majority of this work has largely been carried out in temperate systems and, until recently, has examined the effects of habitat fragmentation on survival. In contrast, we looked at the effect of forest fragmentation on apparent survival of individuals of the white-ruffed manakin (*Corapipo altera*) in southern Costa Rica. Survival and recapture rates were estimated using mark-recapture analyses, based on capture histories from 1993 to 2006. We sampled four forest patches ranging in size from 0.9 to 25 ha, and four sites in the larger 227 ha Las Cruces Biological Station Forest Reserve (LCBSFR). We found a significant difference in annual adult apparent survival rates for individuals marked and recaptured in forest fragments vs. individuals marked and recaptured in the larger LCBSFR (χ^2 = 5.022; df =1; P= 0.025). Contrary to our expectation, survival and recapture probabilities did not differ between male and female manakins. Also, there was no support for the existence of annual variation in survival within each study site. Our results suggest that forest fragmentation is likely having an effect on population dynamics for the white-ruffed manakin in this landscape. Therefore, populations that appear to be persisting in fragmented landscapes might still be at risk of local extinction, and conservation action for tropical birds should be aimed at identifying and reducing sources of adult mortality. Future studies in fragmentation effects on reproductive success and survival, across broad geographical scales, will be needed

before a clear understanding of the effects of habitat fragmentation on populations can be achieved for both tropical and temperate regions.

Introduction

A primary research objective in population ecology has been to link environmental features, such as habitat characteristics, with demographic parameters of populations (Bender et al., 1998; Matthysen et al., 1995; Melbourne et al., 2004; Nichols et al., 1981; Reed, 2004). In the last few decades, a principal focus of research in this field has been on the effect of habitat fragmentation on the relative fitness of wildlife populations (Andren, 1994; Bender et al., 1998; Blake and Karr, 1987; Hanski and Gaggiotti, 2004). Although forest fragmentation can adversely influence both reproductive success (Donovan et al., 1997; Lloyd et al., 2005; Robinson et al., 1995; Tewksbury et al., 2006) and survival (Horak and Lebreton, 1998; Matthysen, 1999), most avian studies have focused on the former because accurately estimating survivorship is logistically challenging (Clobert and Lebreton, 1991; Lampila et al., 2005). Nichols et al. (1981) and Clobert and Lebreton (1991) argued that survival estimates from older studies were not precise and were biased, primarily because recapture rates were assumed to be accurate indices of survival rates, even though potential variation in recapture probabilities were not taken into account. Additional bias was also attributed to a failure to control for other sources of heterogeneity in survival rates, like sex, age class, and breeding status, although recent studies have accounted for these potential effects in their analysis (Sandercock et al., 2000; Sillett and Holmes, 2002).

Methods are now available to accurately estimate a range of demographic parameters, including survival (Karr et al., 1990; Lebreton et al., 1992; Martin et al., 1995; Nichols et al., 1981), although Lampila et al. (2005) found these methods are seldom applied to studies on the effects of habitat fragmentation on survival. Bayne and Hobson (2002) looked at both survival and reproductive success of male ovenbird (*Seiurus aurocapillus*) populations in continuous versus fragmented boreal forests in west-central Canada. They concluded that low reproductive success in smaller forest fragments led to greater dispersal rates out of the fragments, in agreement with previous findings that site fidelity is highly correlated with reproductive success in migratory birds (Bollinger and Gavin, 2004; Haas, 1997; Sedgwick, 2004). Therefore, they concluded that lower local adult survival rates found in smaller forest fragments were not a product of increased mortality, but an artifact of higher emigration rates out of these fragments (Bayne and Hobson, 2002). Survival estimates could also have been confounded with mortality during migration, because they focused on a migratory bird (Doherty and Grubb, 2002). Doherty and Grubb (2002), in contrast, focused on four resident temperate forest birds, and found increased survival in larger forest fragments for the Carolina chickadee (*Poecile carolinensis*), but failed to find an effect for the remaining species.

A lack of consistency in these results could also be an artifact of the relative unimportance of fragmentation effects on breeding bird survival in temperate North America, where pairing success and nest parasitism have already been identified as the two main demographic variables most sensitive to habitat fragmentation in birds (Lampila et al., 2005). What we do not know is what other demographic variables are most affected in other geographical regions, because most research on the effects of fragmentation has taken place in temperate systems.

Observed differences in life history strategies between temperate and tropical systems indicate potential differences in the demographic responses of populations to fragmentation effects. In tropical regions, certain vertebrate taxa, including terrestrial birds, are thought to be long-lived, have low fecundity, and low reproductive success (Martin, 2004; Ricklefs, 1976; Wikelski et al., 2003). For these tropical populations, small decreases in annual adult survival rates could result in a significant reduction of individual lifetime reproductive success, altering population growth rates (Bennett and Owens, 2002; Knutson et al., 2006). Therefore, any effects of habitat fragmentation on survival of birds are likely to have more pronounced effects on tropical than on temperate species.

The white-ruffed manakin (*Corapipo altera)* is a logical candidate to examine the effects of habitat fragmentation on survival rates of tropical species. White-ruffed manakins are long-lived, resident forest birds; the oldest male we have on record is at least 9 yrs old, and we have documented several females to be at least 8 yrs old (V. Ruiz-Gutierrez, *unpublished data*; (Stiles and Skutch, 1989). Manakins are also a lekking species, and survival of individuals is expected to be highly dependent on the quality of proximate feeding sources (Hoglund and Robertson, 1990; Ryder et al., 2006; Snow, 1962). Therefore, we expect to see habitat fragmentation effects on survival rates of adult manakins if habitat quality is lower in forest fragments than in continuous forest sites. According to the resource concentration hypothesis (Root, 1973), larger continuous forest sites are likely to have more available resources than forest fragments**,** and to not be as susceptible to edge and fragmentation effects (Bierregaard et al., 1992; Debinski and Holt, 2000).

The effect of forest fragmentation on manakin survival is likely to be influenced by the sex of the individual, given that female manakins are more mobile than male manakins in this lek breeding system (Hoglund and Alatalo, 1995; Ryder et al., 2006; Sandercock et al., 2000), and higher mobility might increase mortality, especially in disturbed landscapes (Fahrig, 2002). Male white-ruffed manakins also take several years to fully develop reproductive plumage, and females likely reproduce during their first year, thus bearing the costs of reproduction at an earlier age (Devries et al., 2003; Nur, 1988).

In this paper, we look at the effect of forest fragmentation on annual adult survival rates of white-ruffed manakins on the southwestern Pacific side of Costa Rica, using mark-recapture analyses to partition variation in apparent survival and recapture rates as well as to account for differences between the sexes. To the best of our knowledge, this is the first long-term, multi-site study to test for habitat-fragmentation effects on survival of birds in a tropical region, providing a much-needed baseline for comparison with temperate regions (Dhondt and Matthysen, 1993; Githiru and Lens, 2006; Lampila et al., 2005; Pearce-Higgins et al., 2007).

Materials and Methods

Study sites and species

Research was carried out at the Las Cruces Biological Station Forest Reserve, Costa Rica and vicinity (LCBSFR; 8° 47¨ N, 82° 57¨ W) of the Organization for Tropical Studies (Fig. 1). The landscape surrounding the study forest fragments was converted from forest primarily to pasture in the 1940's and 50's, although small coffee farms mixed with banana and *Erythrina sp.* trees, and small garden plots, are also common (Borgella and Gavin, 2005). The landscape surrounding the focal forest fragments has not changed substantially since the study began. All fragments have canopy trees and remnant primary forest vegetation, and are classified as tropical and subtropical evergreen rainforest. The LCBSFR is the main forest fragment in this study (227-ha), although larger tracts of forest also exist in the vicinity (~10 km).

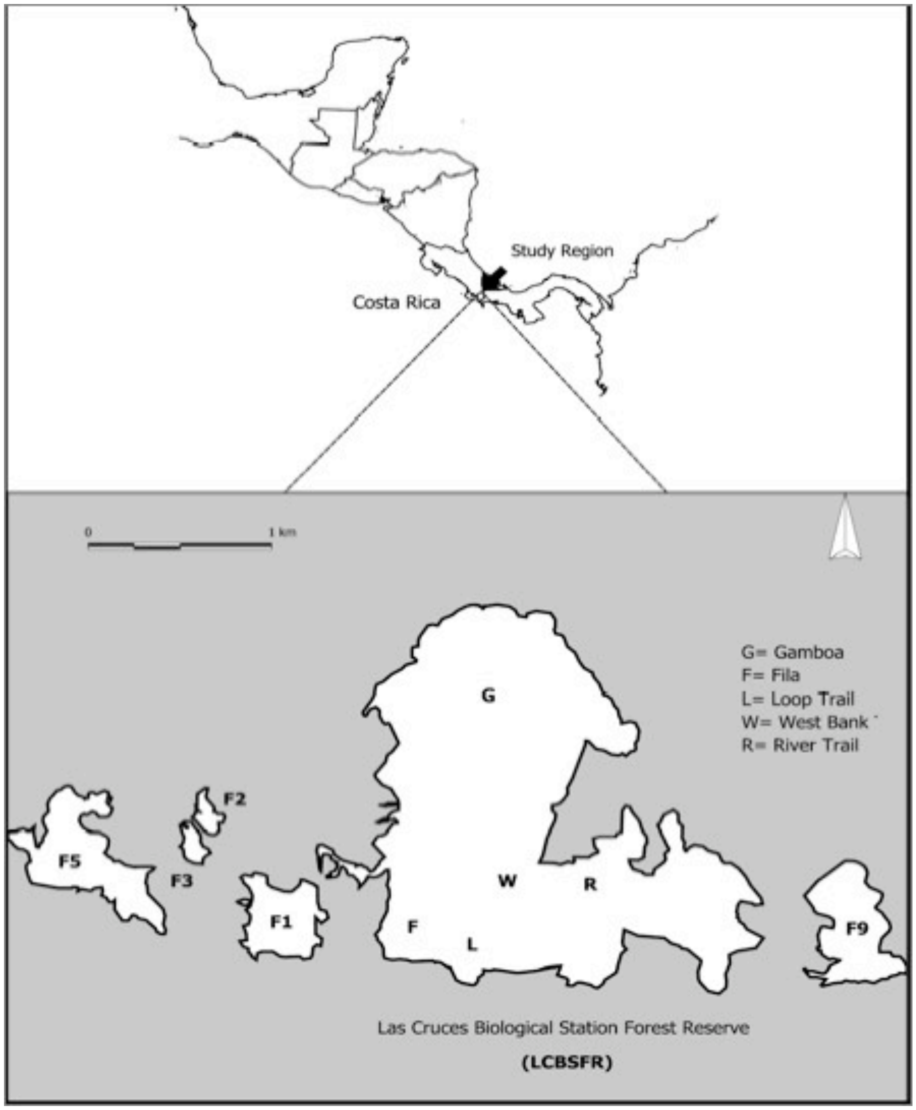

Figure 1. Map of the study sites surround the Las Cruces Biological Station Forest Reserve (LCBSFR), in our study region of San Vito, Costa Rica, based on 1998 aerial photographs. Numbers (F1-F9) correspond to forest fragments, and letters (G,F,L,W,R) to sites within the LCBSFR. The habitat surrounding these fragments is primarily cattle pasture, with some small coffee farms around F9.

The four focal forest fragments in our study range in size from *ca* 0.9 to 25 ha, and *ca* 1278 to 1328 m in elevation, and they are designated Fragment 1 (10 ha), Fragment 2 (0.9 ha), Fragment 5 (20 ha), Fragment 9 (20 ha) (Fig. 1). We also conducted work at five separate sites within the larger LCBSFR: Fila, Gamboa, West Bank Trail, River, and Loop Trail (see inset Fig. 1). A more detailed description of the study area are given in Borgella et al. (2001) and Borgella and Gavin (2005).

Capture methods

We sampled birds by running 20 standard mist nets (2 x 9 m, four shelf, 32-mm mesh) simultaneously. On trapping dates, nets were opened by 0600h, checked for captured birds every 30min, and closed at 1100h. The nets were placed as randomly as the broken terrain allows along a grid of trails. All birds were banded with numbered aluminum bands, and sex and age (if possible) determined on the basis of plumage or presence of a brood patch/cloacal protuberance. If the bird showed any signs of a brood patch, it was identified as a female. If the bird showed any sings of male plumage, like symmetrical blue-black feathers in the wings or face, and a white ruff, it was classified as a male.

Survival analysis

We used capture-mark-recapture analyses for open populations to fit a set of Cormack-Jolly-Seber (CJS) models (Lebreton et al, 1992; notations following Cooch and White (2006). These models, varying in their assumptions of apparent survival (Φ_A) and capture probabilities (ρ), were fit to our data using Program MARK (White and Burnham, 1999). In this paper, our survival estimates are in reality estimates of apparent survival (Φ_A), which is the product of true survival (Φ_T) and site fidelity (F). However, we believe that our estimates of apparent survival are indicative of true survival rates. Permanent emigration rates are believed to be low for tropical species overall, and even more so in long-lived, year-round territorial species with high adult survivorship (Gill and Stutchbury, 2006; Jones et al., 2004; Karr et al., 1990). Directional movement probabilities (ψ) for the white-ruffed manakin in the same study sites did not differ significantly for movements from a small to a large fragment and vice versa ($\psi = 0.08 \pm 0.023$ SE and $\psi = 0.022 \pm 0.009$ SE respectively) (R. Borgella and T.A. Gavin, *unpublished data*). Therefore, we believe our estimates were not biased by differences in emigration rates between small and larger forest patches.

We used time since marked (TSM) models to correct for potential effects of transient individuals on estimates of Φ_A and ρ probabilities (Pradel et al., 1997). These models (referred to as *a2*) separate Φ during the first year after banding (Φ^1) from Φ during subsequent years (Φ^{2+}) (Cooch and White, 2006). These TSM models have been successfully applied in previous work with tropical bird populations to correct for effects of transients and young individuals, for which Φ and ρ probabilities are both known to be underestimated if left uncorrected (Blake and Loiselle, 2002; Johnston et al., 1997; Pearce-Higgins et al., 2007; Sandercock et al., 2000). Recapture probability can vary with time for various reasons, including unequal sampling effort, so we also included time-dependent models (t) for capture probabilities (ρ).

We tested for overdispersion of data by using the goodness-of-fit test that estimates a variation inflation factor ($\hat{c}$) calculated in Program MARK. The estimated value was used to adjust subsequent estimates and statistics if $\hat{c} > 1$, but left as one if $\hat{c} \leq 1$. When $\hat{c}$ was adjusted, model selection was based on Akaike's Information Criterion for small sample sizes using the quasi-likelihood modified criteria (QAICc). Otherwise, just AICc values were used for model selection. Models with ΔAIC_c

values differing by less than 2 were considered equally parsimonious with the best supported model ($\Delta AIC_c = 0$).

Because all models have a degree of validity, we used model averaging procedures to generate model estimates from the entire model set (White and Burnham, 1999). The parameter estimates from each model are weighed by Akaike weights of that model, which represent how well the data support a model, relative to all the other models in the set. The model-averaged estimates come with standard errors that take into account not only within-model uncertainty, but additional uncertainty about which model best characterizes the true biological process being tested.

Model set for sex-related variation in survival

Estimation of differences in survival between sex groups using mark-recapture analysis has proven to yield positively biased estimates when sex is not always known (Nichols et al., 2004). Nichols et al. (2004) argued that most analyses use capture histories from only known-sex individuals, whose sex is usually determined during subsequent captures and, therefore, the investigator's ability to correctly assign sex is dependent on how many times an individual bird is captured. For this reason, only capture histories of male and female individuals using sex known at first capture were used to test for sex-specific survival differences (Nichols et al., 2004). We first grouped individuals into three groups based on sex at first capture: males (M), females (F) and unknown (U). None of the sites had enough unknown individuals to include them as a group in the analysis, so only F and M were tested for group effects on survival (S). We used only a subset of study sites (Fragments 1, 5, 9, and Gamboa and Rio Java in LCBSFR) that had sufficient known male and female capture histories to test for these effects (> 30 captures for each sex). Due to the fact that male and female manakins differ in their movement patterns (Johnston et al., 1997; McDonald, 1993), we also tested sex effects for capture probabilities. We used the procedures outlined above in program MARK to generate a time-since-marked (TSM: a2-t/t) model, with time dependency (t) and sex effects (S) on survival (Φ) and recapture probabilities (ρ) that was used as our global model: Φ (Sa2-t/t) ρ (St).

Model set for survival estimates

We determined if apparent annual survival of white-ruffed manakins was affected by forest fragmentation by grouping all capture histories of males, females, and unknowns and analyzed each separately by study site because not all sites were sampled equally. We used a TSM model (a2-t/t) with time dependency (t) on survival (Φ) and recapture probabilities (ρ) as our global model: Φ (a2-t/t) ρ (t).

Effect of fragmentation on survival rates

To test if there was a difference in apparent survival for individuals captured in forest fragments versus a larger tract of continuous forest, we separated apparent survival estimates generated using model averaging techniques in Program MARK (see *Materials and Methods* above), weighted by the degree of uncertainty in the estimates, into two groups: Fragments and Forest. We used program CONTRAST to test for differences in apparent survival between the groups (Sauer and Hines, 1989).

Results

Apparent survival of males and females

We analyzed 1,294 captures from 513 individuals marked and recaptured between 1993-2000 and 2004-2006 from a subset of five study sites that had enough captures of known-sex birds. Our estimates of overdispersion were $\hat{c} < 1.12$ for all sites, indicating minor overdispersion in the data. None of the best-supported models (AIC weights 0.59-0.86) for the study sites included an effect of sex (S) on probabilities of apparent survival. Only in three of the five sites (Fragment 1, Fila and Gamboa) did a model with a sex effect on apparent survival have at least 10% support (AIC weights 0.13, 0.12, 0.24) (Table 1). For both males and females, survival was constant across years {Φ (.)}, and only the Fila site in LCBSFR showed support for models allowing transients and/or young individuals to vary in survival { Φ (a2-t/t) }(Table 2). Model-averaged estimates for annual apparent survival probabilities for males and females ranged from 0.72 (±0.42 SE) to 0.99 (±0.016 SE) across sites (Table 3). Capture probabilities did not vary between sexes (Table 2), and were time-dependent {ρ (t)} in all but one site, reflecting our unequal sampling effort among years (Table 2 and Appendix E). Capture probabilities for both males and females ranged from 0.06 (±0.15 SE) to 0.91 (±0.08 SE) across sites (Table 2).

Apparent survival and fragmentation

We analyzed 1,419 captures from 792 individuals marked and recaptured from 1993-2000 and 2004-2006. Because there was not a significant difference in apparent survival or capture probabilities between male and female manakins, we used capture histories from all male, female, and unknown sex individuals marked and recaptured for the analysis. Birds were not trapped at each site every year, and hence our reported annual apparent survival estimates were interpolated over longer periods.

We excluded results from the Gamboa site from subsequent analysis because capture probabilities varied widely across the three sampling occasions for this site, including two of the three intervals showing very low recapture probabilities. Therefore, we did not feel the estimates could be reliably compared with other sites.

Both constant {Φ (.)} and time since marking {Φ (a2-./.)} models were

Table 1. Models with at least 10% support used to test for effects of sex (**S**) on apparent survival probabilities of adult white-ruffed manakins in the region surrounding the Las Cruces Biological Station, Costa Rica. Columns give site, model notation with best supported model in bold, number of parameters (**K**), the difference in Akaike's Information Criterion value from the best fit model (**AICcΔ**), and AICc weights (**W**$_i$). Either constant (**Φ{.}**) or time since capture (**Φ{a2-./.}**) models for apparent survival probabilities were best supported. Both constant (**ρ{.}**) and time dependent (**ρ{t}**) models were supported for capture probabilities. Models highlighted in bold represent the best supported model.

Site	Model	K	ΔAIC$_c$	W$_i$
Fragment 1	**Φ{.}ρ{t}**	7	0	0.84
	Φ{Sa2-./.}ρ{t}	10	3.67	0.13
Fragment 5	**Φ{.}ρ{.}**	10	0	0.75
	Φ{a2-./.}ρ{t}	11	2.17	0.25
Fragment 9	**Φ{.}ρ{t}**	6	0	0.59
	Φ{.}ρ{.}	2	1.6	0.26
Fila	**Φ{a2-./.}ρ{t}**	8	0	0.86
	Φ{Sa2-./.}ρ{t}	10	2.1	0.12
Gamboa	**Φ{.}ρ{.}**	2	0	0.68
	Φ{Sa2-./.}ρ{.}	3	2.1	0.24

Table 2. Adult annual apparent survival probabilities for male and female white-ruffed manakins in the region surrounding the Las Cruces Biological Station, Costa Rica, from 1993-2006. Columns give site, sex, individuals per sex (**N**), number of captures (**C**), and model-averaged probabilities of survival (**Φ**) and recapture rates (**P**) for each study site with 1 SE in parentheses. For sites that had time dependent capture probabilities, the range of annual recapture probabilities was provided.

Site	**Sex**	**N**	**Captures**	**Φ (SE)**	**P (SE)**
Fragment 1	M	35	86	0.74 (0.069)	0.17 (0.07) - 0.65 (0.12)
	F	40	107	0.74 (0.081)	
Fragment 5	M	46	108	0.72 (0.042)	0.11 (0.12) - 0.91 (0.08)
	F	59	148	0.72 (0.042)	
Fragment 9	M	68	109	0.74 (0.113)	0.10 (0.09) - 0.33 (0.31)
	F	48	94	0.74 (0.102)	
Fila	M	41	72	0.90 (0.084)	0.12 (0.06) - 0.71 (0.12)
	F	51	91	0.91 (0.083)	
Gamboa	M	59	96	0.99 (0.016)	0.06 (0.15)
	F	66	76	0.98 (0.09)	

Table 3. Models with at least 10% support used to generate apparent survival probabilities of adult white-ruffed manakins in the region surrounding the Las Cruces Biological Station, Costa Rica, from 1993 to 2006. Columns give site, forest patch size (ha), model notation with the best supported model in bold, number of parameters (**K**), Akaike's Information Criterion values (**AICc**), and AICc weights (**W*i***). Either constant (**Φ{.}**) or time since capture (**Φ{a2-./.}**) models for survival probabilities were best supported. Both constant (**ρ{.}**) and time dependent (**ρ{t}**) models were supported for capture probabilities.

Site	Size (ha)	Model	K	AICc	W_i
Fragment 2	0.9	**Φ{.}ρ{.}**	2	85.34	0.77
		Φ{a2-./.}ρ{.}	3	87.71	0.23
Fragment 1	10	**Φ{.}ρ{t}**	7	260.74	0.67
		Φ{a2-./.}ρ{t}	8	262.37	0.29
Fragment 9	20	**Φ{.}ρ{.}**	2	164.77	0.67
		Φ{a2-./.}ρ{t}	7	166.90	0.23
Fragment 5	25	**Φ{.}ρ{t}**	10	291.22	0.76
		Φ{.}ρ{.}	2	294.65	0.14
Fila	227	**Φ{a2-./.}ρ{.}**	3	214.71	0.55
		Φ{a2-./t}ρ{.}	8	215.96	0.29
		Φ{.}ρ{.}	2	217.51	0.14
Gamboa	227	**Φ{.}ρ{.}**	2	117.11	0.61
		Φ{a2-./.}ρ{.}	3	117.22	0.21
		Φ{a2-./t}ρ{.}	5	118.46	0.11
West Bank Trail	227	**Φ{.}ρ{t}**	4	69.08	0.44
		Φ{.}ρ{.}	2	69.76	0.31
		Φ{a2-./.}ρ{.}	3	71.95	0.10
River	227	**Φ{.}ρ{.}**	2	70.21	0.60
		Φ{a2-./.}ρ{.}	3	71.33	0.34
Loop Trail	227	**Φ{.}ρ{t}**	3	40.12	0.63
		Φ{.}ρ{.}	2	41.76	0.27

supported for apparent survival probabilities for the remaining sites (Table 3). There was no support for annual variation in survival for any of the sites. In all four fragments the best supported model was the Φ (.) model, while in 3 of the 4 fragments the Φ (a2-./.) model was also supported with weights between 0.23 and 0.29 (Table 3). Similarly, in all four sites within the larger forest the constant survival {Φ (.)} model was best supported, while in 3 of the 4 sites the time-since marking model Φ (a2-./.) was also supported with Akaike weights of 0.10 and 0.34 (Table 3).

Our model-averaged estimates of apparent survival ranged from Φ= 0.64 (±0.005 SE) to 0.75 (± 0.08) for the sites in forest fragments, and from Φ= 0.76 (±0.11 SE) to 0.97 (±0.15 SE) for the sites in the larger forest tract of the LCBSFR (Table 4). Capture probabilities were constant { ρ (.)} or time-dependent { ρ (t)} in the best supported model for all sites. Estimates for recapture probabilities varied between 0.11 (±0.07 SE) to 0.97 (±0.12 SE). Apparent survival estimates for individuals captured in the four forest fragments were significantly different from individuals captured in the sites within the larger LCBSFR (χ^2 = 5.0220; df =1; P= 0.025).

Discussion

Survival and fragmentation

Although it is widely accepted that habitat fragmentation has a negative effect on survival, to the best of our knowledge, this is the first long-term, multi-site study to test for these effects in a tropical region. We found that annual adult survival rates of the white-ruffed manakin in southwestern Costa Rica were significantly lower for individuals marked and recaptured in forest fragments, when compared to individuals captured in a larger tract of forest. Although we acknowledge that survival rates vary geographically, we do not believe that the effect of forest fragmentation on survival is a product of this variation.

Table 4. Adult annual apparent survival probabilities for white-ruffed manakins in the region surrounding the Las Cruces Biological Station, Costa Rica, from 1993-2006. Columns give site, total individuals (**N**), capture histories, and model-averaged probabilities of survival (**Φ**) and recapture rates (**P**) for each study site with 1 SE in parentheses. For sites that had time dependent capture probabilities, the range of annual recapture probabilities was provided.

Site	**N**	**Captures**	**Φ (SE)**	**P (SE)**
Fragment 2	26	56	0.72 (0.11)	0.31 (0.11)
Fragment 1	91	216	0.75 (0.08)	0.19 (0.12) - 0.64 (0.13)
Fragment 9	167	272	0.72 (0.11)	0.23 (0.12)
Fragment 5	131	287	0.64 (0.05)	0.23 (0.25) - 0.97 (0.12)
Fila	92	178	0.76 (0.11)	0.45 (0.11)
West Bank Trail	63	75	0.97 (0.15)	0.09 (0.08) – 0.10 (0.08)
River	41	48	0.91 (0.15)	0.11 (0.07)
Loop Trail	54	78	0.94 (0.15)	0.41 (0.21)

Our results were not confounded by potential effects of mortality during migration, and hence we believe that reduced survivorship in forest fragments is not an artifact of higher emigration rates out of smaller fragments, in contrast to Bayne and Hobson (2002). By using a resident tropical forest bird, we also did not have site fidelity correlated with reproductive success in our study species. Although white-ruffed manakins are known to show altitudinal movements in the Caribbean slope of the country, individuals in our Pacific slope study site appear to have year-round territories, with individuals recaptured both during the breeding and non-breeding season at the same sites, and even in the same net lanes (V. Ruiz-Gutierrez, *unpublished data*). Further, work by Borgella and Gavin (*unpublished data*) carried out in the same study site has shown that the probability of directional movement for the white-ruffed manakin is not dependent on fragment size, indicating that it is unlikely that there are higher emigration rates in the smaller forest fragments.

The mechanisms underlying reduced survivorship for individuals in smaller fragments are probably habitat related. This highly frugivorous lekking species is likely to be affected by a decrease in the availability or quality of food resources in smaller fragments (Ryder et al., 2006). Other factors might include increased mortality in the habitat matrix surrounding the forest fragments during movement or foraging, as well as differences in predation rates between forest fragments and larger continuous forest. Also, normally patchy frugivorous resources might not be as constant and be spaced further apart in fragmented landscapes when compared to more continuous habitats. Therefore, manakins may be foraging over larger distances to find resources in fragmented habitats, and potentially experiencing increased mortality due to increased movement through the inhospitable matrix.

Regardless of the underlying mechanisms, it is clear that forest fragmentation, through its impact on survival, is likely driving population dynamics of white-ruffed manakins in this region (Knutson et al., 2006). This bird species, like many other tropical species, is long-lived, has low reproductive success and small clutch sizes (Bennett and Owens, 2002; Martin et al., 2000). Therefore, the detected reduction in annual adult survival rates is likely decreasing individual lifetime reproductive success of white-ruffed manakin individuals, and hence altering population growth rates in our study region (Bennett and Owens, 2002). To accurately determine the nature of the relationship between forest fragmentation and survival, future work will require a broader range of study sites, as well as the inclusion of larger forest tracts in the region.

Sex and survival

No model with sex effects on survival received more than 24% support (Table 1). Our failure to detect a significant difference in survival rates between males and females is contrary to our expectations of higher male survivorship, but in agreement with previous results for the white-collared (*Manacus candei*) and band-tailed (*Pipra fasiicauda*) manakins (Blake and Loiselle, 2002; Pearce-Higgins et al., 2007). However, Blake and Loiselle (2002) did find that survivorship in red-capped manakin females was higher than males.

We based our expectation of higher male survivorship on assumptions related to movement and reproductive costs. A lack of sex effects on survival suggests that the cost of reproduction in females is not significantly higher than the cost of finding, establishing, and defending a lek territory for males. Another plausible explanation is that there might not be a difference in movement between males and females of the white-ruffed manakin in our study region. We found evidence for this in our results given that we found minimal support for models that included sex-effects on capture probabilities. Blake and Loiselle (2002) also found little evidence to suggest that movement varies between sexes for the white-ruffed manakin based on their analysis of dispersal distances.

Survival of Tropical Birds

Our estimates of apparent survival, Φ= 0.74 (±0.069 SE) to 0.97 (±0.15 SE), are some of the highest recorded not just for Pipridae, but also for any resident tropical bird using rigorous methodology (Karr et al. 1990; Brawn et al, 1995; Johnston et al, 1997; Blake and Loiselle 2002; Pearce-Higgins, 2007). Johnston et al (1997) estimated survival for several Pipridae species, with survival ranging from Φ=0.69 (0.05 SE) to 0.74 (0.11 SE). Blake and Loiselle (2002) also estimated survival for several manakin species, with apparent survival Φ = 0.56 (0.19 SE) and Φ = 0.59 (0.18 SE) for the white-ruffed manakins in their breeding and non-breeding sites, respectively (Blake and Loiselle 2002). Recent work by Pearce-Higgins (2007) on band-tailed manakins (*Pipra fasciicauda*) had survival estimates of Φ = 0.673 (0.426-0.861).

Despite our high survival estimates, we believe they only lend partial support for the overall argument of higher survival in tropical vs. temperate avian species, given that we only focused on one population and one species. Survival is also known to vary geographically between populations of the same species (Dhondt, 2001; Frederiksen et al., 2005), and only a long-term, multi-species survivorship analysis across a broader geographical scale could provide enough evidence for comparison with temperate populations.

Conclusions

Following a fragmentation event, species found in the remnant forest fragments have a high probability of local extinction, although certain species remain long past the event (Bierregaard et al., 2001; Ferraz et al., 2007). Our results indicate that for tropical regions, species that appear to be persisting in fragmented landscapes might still be at risk of local extinction. Therefore, conservation efforts for tropical birds should be aimed at identifying and mitigating sources of adult mortality in fragmented landscapes. Future studies of fragmentation effects in multiple areas for individual taxa, which examine both survival and reproductive rates, will also be needed before a clear understanding on the effects of habitat fragmentation on populations can be achieved for both tropical and temperate regions.

REFERENCES

Andren, H. 1994. Effects Of Habitat Fragmentation On Birds And Mammals In Landscapes With Different Proportions Of Suitable Habitat - A Review. Oikos **71**:355-366.

Bayne, E. M., and K. A. Hobson. 2002. Apparent survival of male ovenbirds in fragmented and forested boreal landscapes. Ecology **83**:1307-1316.

Bender, D. J., T. A. Contreras, and L. Fahrig. 1998. Habitat loss and population decline: A meta-analysis of the patch size effect. Ecology **79**:517-533.

Bennett, P. M., and I. P. F. Owens. 2002. Evolutionary Ecology of Birds: Life Histories, Mating Systems and Extinction. Oxford University Press, New York, NY.

Bierregaard, R. O., C. Gascon, T. E. Lovejoy, and R. C. G. Mesquita, editors. 2001. Lessons from Amazonia: The Ecology and Conservation of a Fragmented Landscape. Yale University Press, New Haven, CT.

Bierregaard, R. O., T. E. Lovejoy, V. Kapos, A. A. Dossantos, and R. W. Hutchings. 1992. The Biological Dynamics Of Tropical Rain-Forest Fragments. Bioscience **42**:859-866.

Blake, J. G., and J. R. Karr. 1987. Breeding Birds Of Isolated Woodlots - Area And Habitat Relationships. Ecology **68**:1724-1734.

Blake, J. G., and B. A. Loiselle. 2002. Manakins (Pipridae) in second-growth and old-growth forests: Patterns of habitat use, movement, and survival. Auk **119**:132-148.

Bollinger, E. K., and T. A. Gavin. 2004. Responses of nesting bobolinks (Dolichonyx oryzivorus) to habitat edges. Auk **121**:767-776.

Borgella, R., and T. A. Gavin. 2005. Avian community dynamics in a fragmented tropical landscape. Ecological Applications **15**:1062-1073.

Borgella, R., A. A. Snow, and T. A. Gavin. 2001. Species richness and pollen loads of hummingbirds using forest fragments in southern Costa Rica. Biotropica **33**:90-109.

Clobert, J., and J. D. Lebreton. 1991. Estimation of demographic parameters in bird populations. Pages 75-104 *in* C. M. Perrins and J. D. Lebreton, editors. Population Studies: Their relevance to Conservation and Management. Oxford University Press, Oxford.

Cooch, E. G., and G. White. 2006. Program MARK: A gentle introduction.

Debinski, D. M., and R. D. Holt. 2000. A survey and overview of habitat fragmentation experiments. Conservation Biology **14**:342-355.

Devries, J. H., J. J. Citta, M. S. Lindberg, D. W. Howerter, and M. G. Anderson. 2003. Breeding-season survival of mallard females in the Prairie Pothole Region of Canada. Journal Of Wildlife Management **67**:551-563.

Dhondt, A. A. 2001. Trade-offs between reproduction and survival in Tits. Ardea **89**:155-166.

Dhondt, A. A., and E. Matthysen. 1993. Conservation Biology Of Birds - Can We Bridge The Gap Between Head And Heart. Trends In Ecology & Evolution **8**:160-161.

Doherty, P. F., and T. C. Grubb. 2002. Survivorship of permanent-resident birds in a fragmented forested landscape. Ecology **83**:844-857.

Donovan, T. M., P. W. Jones, E. M. Annand, and F. R. Thompson. 1997. Variation in local-scale edge effects: Mechanisms and landscape context. Ecology **78**:2064-2075.

Fahrig, L. 2002. Effect of habitat fragmentation on the extinction threshold: A synthesis. Ecological Applications **12**:346-353.

Ferraz, G., J. D. Nichols, J. E. Hines, P. C. Stouffer, R. O. Bierregaard, and T. E. Lovejoy. 2007. A large-scale deforestation experiment: Effects of patch area and isolation on Amazon birds. Science **315**:238-241.

Frederiksen, M., M. P. Harris, and S. Wanless. 2005. Inter-population variation in demographic parameters: a neglected subject? Oikos **111**:209-214.

Gill, S. A., and B. J. M. Stutchbury. 2006. Long-term mate and territory fidelity in neotropical buff-breasted wrens (Thryothorus leucotis). Behavioral Ecology And Sociobiology **61**:245-253.

Githiru, M., and L. Lens. 2006. Annual survival and turnover rates of an afrotropical robin in a fragmented forest. Biodiversity And Conservation **15**:3315-3327.

Haas, C. A. 1997. What characteristics of shelterbelts are important to breeding: Success and return rate of birds? American Midland Naturalist **137**:225-238.

Hanski, I., and O. Gaggiotti, editors. 2004. Ecology, genetics, and evolution of metapopulations. Elsevier Academic Press, Amsterdam.

Hoglund, J., and R. V. Alatalo. 1995. Leks. Princeton University Press, Princeton, New Jersey.

Hoglund, J., and J. G. M. Robertson. 1990. Spacing Of Leks In Relation To Female Home Ranges, Habitat Requirements And Male Attractiveness In The Great Snipe (Gallinago-Media). Behavioral Ecology And Sociobiology **26**:173-180.

Horak, P., and J. D. Lebreton. 1998. Survival of adult Great Tits Parus major in relation to sex and habitat; a comparison of urban and rural populations. Ibis **140**:205-209.

Johnston, J. P., W. J. Peach, R. D. Gregory, and S. A. White. 1997. Survival rates of tropical and temperate passerines: A Trinidadian perspective. American Naturalist **150**:771-789.

Jones, J., J. J. Barg, T. S. Sillett, M. L. Veit, and R. J. Robertson. 2004. Minimum estimates of survival and population growth for cerulean warblers (Dendroica Cerulea) breeding in Ontario, Canada. Auk **121**:15-22.

Karr, J. R., J. D. Nichols, M. K. Klimkiewicz, and J. D. Brawn. 1990. Survival Rates Of Birds Of Tropical And Temperate Forests - Will The Dogma Survive. American Naturalist **136**:277-291.

Knutson, M. G., L. A. Powell, R. K. Hines, M. A. Friberg, and G. J. Niemi. 2006. An assessment of bird habitat quality using population growth rates. Condor **108**:301-314.

Lampila, P., M. Monkkonen, and A. Desrochers. 2005. Demographic responses by birds to forest fragmentation. Conservation Biology **19**:1537-1546.

Lebreton, J. D., K. P. Burnham, J. Clobert, and D. R. Anderson. 1992. Modeling Survival And Testing Biological Hypotheses Using Marked Animals - A Unified Approach With Case-Studies. Ecological Monographs **62**:67-118.

Lloyd, P., T. E. Martin, R. L. Redmond, U. Langner, and M. M. Hart. 2005. Linking demographic effects of habitat fragmentation across landscapes to continental source-sink dynamics. Ecological Applications **15**:1504-1514.

Martin, T. E. 2004. Avian life-history evolution has an eminent past: Does it have a bright future? Auk **121**:289-301.

Martin, T. E., J. Clobert, and D. R. Anderson. 1995. Return rates in studies of life history evolution: Are biases large? Journal Of Applied Statistics **22**:863-875.

Martin, T. E., P. R. Martin, C. R. Olson, B. J. Heidinger, and J. J. Fontaine. 2000. Parental care and clutch sizes in North and South American birds. Science **287**:1482-1485.

Matthysen, E. 1999. Nuthatches (Sitta europaea : Aves) in forest fragments: demography of a patchy population. Oecologia **119**:501-509.

Matthysen, E., L. Lens, S. Vandongen, G. R. Verheyen, L. A. Wauters, F. Adriaensen, and A. A. Dhondt. 1995. Diverse Effects Of Forest Fragmentation On A Number Of Animal Species. Belgian Journal Of Zoology **125**:175-183.

McDonald, D. B. 1993. Demographic Consequences Of Sexual Selection In The Long-Tailed Manakin. Behavioral Ecology **4**:297-309.

Melbourne, B. A., K. F. Davies, C. R. Margules, D. B. Lindenmayer, D. A. Saunders, C. Wissel, and K. Henle. 2004. Species survival in fragmented landscapes: where to from here? Biodiversity And Conservation **13**:275-284.

Nichols, J. D., W. L. Kendall, J. E. Hines, and J. A. Spendelow. 2004. Estimation of sex-specific survival from capture-recapture data when sex is not always known. Ecology **85**:3192-3201.

Nichols, J. D., B. R. Noon, S. L. Sokes, and J. E. Hines. 1981. Remarks on the use of mark-recapture methodology in estimating avian population size. Studies in Avian Biology **6**:121-136.

Nur, N. 1988. The Cost Of Reproduction In Birds - An Examination Of The Evidence. Ardea **76**:155-168.

Pearce-Higgins, J. W., R. C. Brace, and J. Hornbuckle. 2007. Survival of Band-tailed Manakins. Condor **109**:167-172.

Pradel, R., J. E. Hines, J. D. Lebreton, and J. D. Nichols. 1997. Capture-recapture survival models taking account of transients. Biometrics **53**:60-72.

Reed, D. H. 2004. Extinction risk in fragmented habitats. Animal Conservation **7**:181-191.

Ricklefs, R. E. 1976. Growth-Rates Of Birds In Humid New World Tropics. Ibis **118**:179-207.

Robinson, S. K., F. R. Thompson, T. M. Donovan, D. R. Whitehead, and J. Faaborg. 1995. Regional Forest Fragmentation And The Nesting Success Of Migratory Birds. Science **267**:1987-1990.

Root, R. B. 1973. Organization Of A Plant-Arthropod Association In Simple And Diverse Habitats - Fauna Of Collards (Brassica-Oleracea). Ecological Monographs **43**:95-120.

Ryder, T. B., J. G. Blake, and B. R. A. Loiselle. 2006. A test of the environmental hotspot hypothesis for lek placement in three species of Manakins (Pipridae) in Ecuador. Auk **123**:247-258.

Sandercock, B. K., S. R. Beissinger, S. H. Stoleson, R. R. Melland, and C. R. Hughes. 2000. Survival rates of a neotropical parrot: Implications for latitudinal comparisons of avian demography. Ecology **81**:1351-1370.

Sauer, J. R., and J. E. Hines. 1989. Wildlife Software - Testing For Differences Among Survival Or Recovery Rates Using Program Contrast. Wildlife Society Bulletin **17**:549-550.

Sedgwick, J. A. 2004. Site fidelity, territory fidelity, and natal philopatry in willow flycatchers (Empidonax traillii). Auk **121**:1103-1121.

Sillett, T. S., and R. T. Holmes. 2002. Variation in survivorship of a migratory songbird throughout its annual cycle. Journal Of Animal Ecology **71**:296-308.

Snow, D. W. 1962. A field study of the Black and White Manakin, *Manacus manacus*, in Trinidad. Zoologica: New York Zoological Society:65-104.

Stiles, F. G., and A. F. Skutch. 1989. A Guide to the Birds of Costa Rica. Cornell University Press, Ithaca, NY.

Tewksbury, J. J., L. Garner, S. Garner, J. D. Lloyd, V. Saab, and T. E. Martin. 2006. Tests of landscape influence: Nest predation and brood parasitism in fragmented ecosystems. Ecology **87**:759-768.

White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study **46**:120-139.

Wikelski, M., L. Spinney, W. Schelsky, A. Scheuerlein, and E. Gwinner. 2003. Slow pace of life in tropical sedentary birds: a common-garden experiment on four stonechat populations from different latitudes. Proceedings Of The Royal Society Of London Series B-Biological Sciences **270**:2383-2388.

CHAPTER 3

WEAK GENETIC STRUCTURING INDICATES ONGOING GENE FLOW ACROSS WHITE-RUFFED MANAKIN (*Corapipo altera)* POPULATIONS IN A HIGHLY FRAGMENTED COSTA RICA

Abstract

We explored the effects of recent forest fragmentation on fine-scale patterns of population structuring and genetic diversity in populations of White-ruffed Manakins (*Corapipo altera*) inhabiting premontane forest fragments of varying size in southwestern Costa Rica. Habitat fragmentation is a major conservation concern for avian populations worldwide, but studies of the genetic effects of fragmentation on Neotropical birds are limited. We sampled 159 manakins from nine forest fragments of varying size within an 18 kilometer radius and genotyped these birds at 13 microsatellite loci. Bayesian clustering methods revealed that birds from all fragments comprised a single genetic population, and an MCMC approach showed that the fragments were likely to be at migration-drift equilibrium. F-statistics showed only modest levels of differentiation between forest fragments. We calculated allelic diversity indices for each fragment but found no correlation between genetic diversity and fragment size. These results suggest that manakins may retain substantial connectivity via inter-fragment dispersal despite habitat fragmentation.

Introduction

Habitat loss and fragmentation are primary causes of vertebrate population declines and species extinctions (Sala et al. 2003), particularly in the biodiversity-rich Neotropical region (Laurance et al. 2002), where birds have received considerable conservation attention. Habitat fragmentation has been shown to adversely affect bird populations via multiple pathways of causation, from within-fragment changes in food availability (Zanette et al. 2000), microclimate (Karr and Freemark 1983), nesting success (Sieving 1992; Robinson et al. 1995; Robinson et al. 2000), and survivorship (Doherty and Grubb 2002), to reductions in dispersal potential between fragments (Laurance et al. 2004; Laurance and Gomez 2005) that alter population connectivity (Uezu et al. 2005). Fragmentation has led to local extinctions of many species throughout the Neotropics (Kattan 1994; Renjifo 1999; Robinson 1999; Stratford and Stouffer 1999; Ferraz et al. 2007), particularly of forest understory insectivores (Stouffer and Bierregaard 1995; Canaday 1996). A species' ability to disperse through the matrix habitat surrounding forest fragments and thereby maintain connectivity may be the most important determinant of its local population persistence in remnant forest fragments (Castellon and Sieving 2006; Stouffer et al. 2006). Successful mitigation of the adverse effects of fragmentation on Neotropical bird populations thus requires a better understanding of fine-scale and taxon-specific patterns of population connectivity in fragmented landscapes.

Patterns of genetic variation can provide insights into dispersal patterns and population connectivity on scales that direct field measures of dispersal are unable to address (Koenig et al. 1996). Over the course of generations, dispersal limitation may lead to genetic substructuring and a reduction in genetic diversity in isolated fragments (Caizergues et al. 2003), effects that likely pose a threat to the long-term viability of populations (Frankham 1996). Despite the recent application of highly sensitive markers such as microsatellites to examine population structure in many natural populations, we know of no microsatellite-based study that has investigated fine scale genetic structuring in a Neotropical bird that occupies a fragmented landscape. Most previous work on intra-specific genetic differentiation in Neotropical birds has been based instead on lower resolution markers (usually mitochondrial DNA haplotype variation; e.g., Brown et al. 2004) and focused on longer time scales in the context of incipient speciation, exploring effects of landscape features such as rivers (Capparella 1988, 1992), mountains (Brumfield and Capparella 1996), and islands (Ricklefs and Bermingham 2001) on population structure. MtDNA-based studies on the effects of natural forest fragmentation on genetic structure and diversity (Bates 2000, 2002) found limited (if any) effects on genetic structure. Previous work in Southwestern Costa Rica on understory insectivores documents that recent forest fragmentation has led to unstable communities (Borgella and Gavin 2005) and a reduction in mtDNA-based measures of genetic diversity (Brown et al. 2004) for birds in small isolated fragments, suggesting that fragmentation poses a serious threat to forest-dependent avian populations in this part of the world.

Here we apply a set of microsatellite markers to a population of White-ruffed Manakins (*Corapipo altera*) occupying forest remnants of varying size in the recently fragmented Coto Brus region of Southwestern Costa Rica. Once covered in extensive tropical premontane rainforest (Borgella et al. 2001; Borgella and Gavin 2005), the forests of the region have been fragmented by various anthropogenic uses over the past half-century. The White-ruffed Manakin is a common resident of the lower and middle strata of tropical lowland and montane evergreen forests from eastern Honduras to northwestern Colombia (A.O.U. 1998). This manakin species is mainly frugivorous (Skutch 1967; Rosselli 1994), and males display on moss-covered logs arranged in dispersed leks (Slud 1964; Rosselli 2002). Individuals generally inhabit intact forest, but may search for food in nearby clearings (Skutch 1967). We expected genetic differentiation among fragments for this species due to low nesting success for tropical birds in general (Robinson et al. 2000), low rates of colonization of forest fragments by dispersing individuals due to high lek fidelity (Hoglund and Shorey

2003; Borgella and Gavin 2005), and potentially increased mortality in matrix habitats during dispersal events.

Our objectives in this study were to explore genetic patterns at two levels: population structuring across the landscape mosaic of forest fragments, and within-fragment genetic diversities. To assess the connectivity of the manakins occupying these patches, we use Bayesian clustering methods to estimate the number of genetically distinct populations, and F-statistics to examine patterns of gene flow among forest fragments. We calculate allelic diversity indices to test if there is a reduction of genetic diversity with the size of forest fragments. Considered in concert, the results of these analyses suggest that these populations of manakins continue to exhibit substantial connectivity.

Materials and Methods

Study area and sampling design

Birds were sampled from ten mid-elevation tropical forest sites within the Coto Brus region of Southwestern Costa Rica during June-August 2004 and June-August 2006 (Fig. 2). Samples were taken during the breeding season, as resident breeders are most relevant to population genetic structure. This region was originally forested, but the landscape has become increasingly fragmented over the past half-century, creating a matrix of anthropogenically modified non-forest habitats that may be barriers to dispersal for birds inhabiting the remaining forest fragments. Seven fragments representing a range of patch sizes from 1.4 to 35 hectares (ha) were located within a 7 km radius of the Las Cruces Biological Station (LCBS). Forest patch size was determined using the area calculation feature in program MANIFOLD v6 (Manifold.net) by hand-digitizing orthorectified aerial photographs from 1998. Two additional sampling sites were located within the nearby 5,600 ha Guaymi Indigenous

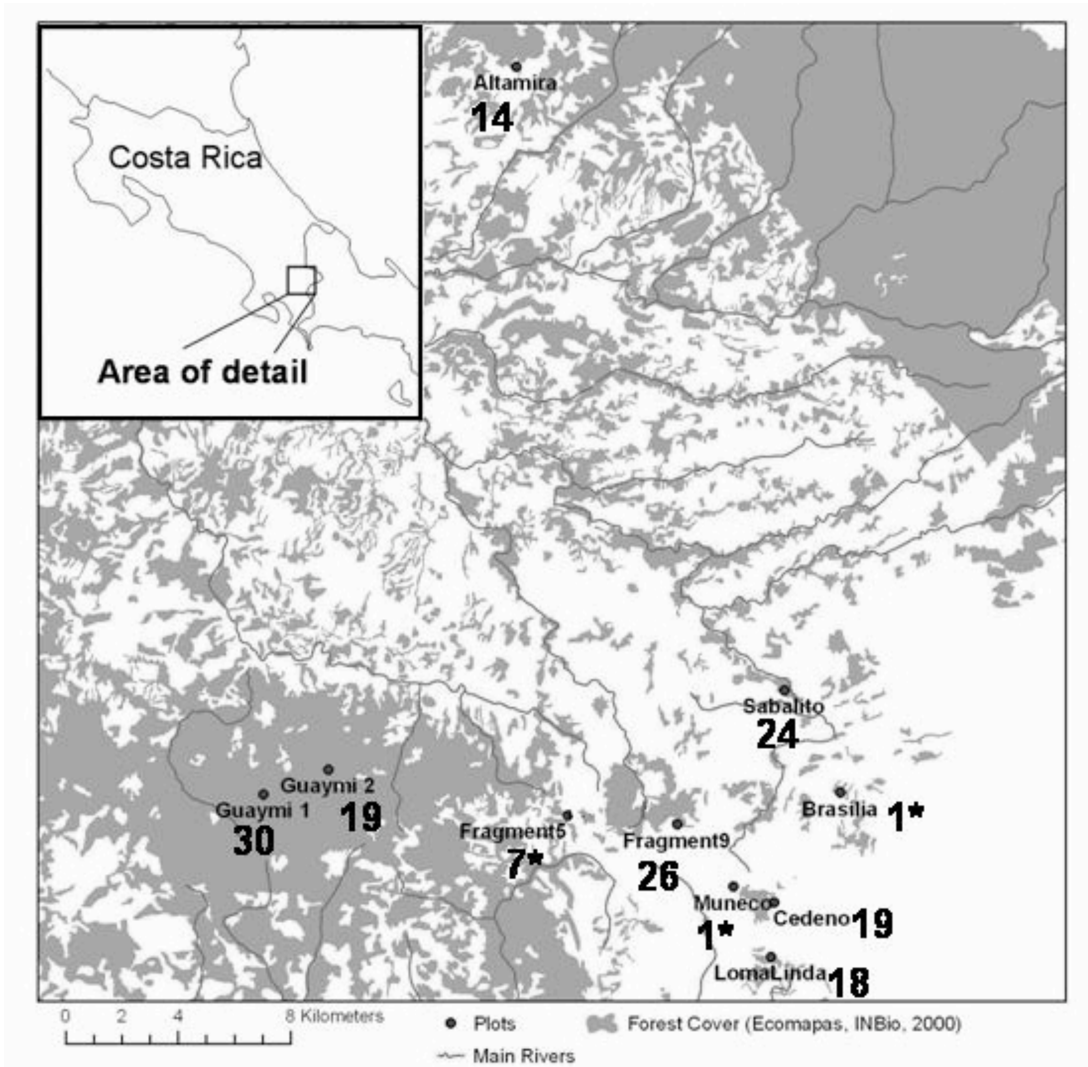

Figure 2. Map of the sampling area, showing the 10 sites where birds were caught and the subsequent sample sizes of genotyped individuals. Asterisks designate sites not included in the Fst and genetic diversity analyses owing to small sample sizes. Gray represents current forest cover and white represents non-forest. Map courtesy of Guillermo Durán and the Las Cruces GIS lab.

Reserve. As these two sample sites were within the same large fragment, the individuals sampled from both Guaymi locations were pooled and treated as a single sample. Anticipating the possibility that differentiation would be low among these nine sites within a 10 km radius, birds were also sampled from one site (Altamira) within the 500,000 ha La Amistad World Biosphere Reserve (Fig. 2), which was about 30 km from the remaining sites. All sites were between 900 and 1300 meters in elevation. At each site, White-ruffed Manakins were captured in mist nets and permanently marked with individually numbered bands as part of a long-term demographic study. Blood samples were taken via brachial venipuncture, and the blood samples were preserved in lysis buffer (2% Sodium dodecyl sulfate, 100mM Tris pH 8.0, 100mM Na_2EDTA, 10 mM NaCl). Birds were then released. All activities involving live birds were conducted under an approved Cornell University Institutional Animal Care and Use protocol (#05-0053).

DNA extraction and genotyping

Genomic DNA was extracted from each blood sample using Perfect gDNA Blood Mini kits (Eppendorf), following the manufacturer's protocol. DNA was eluted in 200 µl of buffer and stored at -20C until used for genotyping. Microsatellite alleles were amplified via the polymerase chain reaction (PCR) using 15 PCR primer pairs designed for *Corapipo altera,* following the protocols detailed in Barnett et al. (in press). Labeled PCR products were analyzed on an ABI Prism 3100 Genetic Analyzer (Applied Biosystems), and allele sizes were estimated using GENEMAPPER™ Vers. 3.7 (Applied Biosystems).

Microsatellite validation and variability

We checked each locus for the presence of null alleles using the program MICRO-CHECKER version 2.2.3 (Van Oosterhout et al. 2004), setting the number of iterations to 10000. Since all analyzed samples amplified at least one allele, we used the Brookfield 1 equation as a null allele estimator. We estimated observed heterozygosities (Hobs) and expected heterozygosities (Hexp) corrected for sampling bias using GENETIX version 4.05.2 (Belkhir et al. 1996-2004). We further tested for the significance of heterozygote deficiency relative to Hardy-Weinberg equilibrium (HWE) in the entire sample. We also tested for the significance of heterozygote deficiency or excess in each sample site, depending on the values estimated for Hobs and Hexp. These tests of deviation from HWE were performed, using the Markov Chain exact test method of GENEPOP version 3.4 (Raymond and Rousset 1995). The default values of the Markov Chain parameters were increased to obtain standard errors lower than 0.01 for the P value estimates. We used 10,000 dememorizations, 150 batches, and 4000 iterations per batch. We also estimated the Fis values within each fragment and tested for their significance using 10,000 permutations in GENETIX.

For each pair of loci, we tested for the presence of linkage disequilibrium with the Markov chain method of GENEPOP (Raymond and Rousset 1995). The default values of the Markov Chain parameters were again increased to obtain standard errors of less than 0.01. We used 10,000 dememorizations, 500 batches, and 5,000 iterations per batch.

When applicable, we controlled for multiple comparisons by calculating the False Discovery Rate (FDR) –adjusted P-values using the compute.fdr function in R 2.4.1 (Ihaka and Gentleman 1996). The library of the function is available online at http://www.stjuderesearch.org/depts/biostats/documents/fdr-library.R. We used the method of Benjamini and Hochberg (1995).

Population structure

We used two Bayesian clustering approaches, GENELAND version 1.0.5 (Guillot et al. 2005a & b) and STRUCTURE version 2.1 (Falush et al. 2003; Pritchard et al. 2000), to explore the population structuring of manakins across this fragmented landscape. Both of these programs use multi-locus genotype information to arrange individuals into groups that most closely fit the expectations of Hardy-Weinberg equilibrium while minimizing linkage disequilibrium. Whereas both GENELAND and STRUCTURE employ similar analytical frameworks, GENELAND has two important differences: first, it allows the number of genetic groups (K) to vary, and second, it allows the spatial coordinates of each sample to be incorporated into the model as a prior. STRUCTURE is currently the most widely adopted method of determining population structure for groups of individuals with unknown population affinities, and thus provides a standard with which to compare the results produced by GENELAND.

In GENELAND, we performed an initial series of runs to determine the number of genetically distinct groups (K). Preliminary runs were performed to adjust the input parameter values so that the Markov chain Monte-Carlo (MCMC) could converge by the end of the runs, as well as to explore the parameter space comprehensively. We then performed 12 runs of 200,000 MCMC iterations each at the selected parameters: minimum number of genetic groups =1, maximum number of genetic groups =50, maximum number of nuclei in the Poisson-Voronoi tessellation = 500, maximum rate of the Poisson process used to generate the Voronoi cells = 500, allele frequency model = Dirichlet. Multiple runs were performed with these parameters to check the consistency of the value inferred for K. The uncertainty associated with the spatial coordinates was set to 400m, based on a 10 ha estimate of home range size in the closely related *C. guttaralis* (Thery 1992), as no estimate of the home range size of *C. altera* is currently available. In a typical GENELAND analysis, the next step is to assign individuals to the K genetic groups; this step was not necessary here, as the estimated number of genetic groups was 1 for each of the 12 runs (see Results).

In our STRUCTURE analyses we performed runs with values of K set from 1 to 8. Five runs were performed for each value of K, to check the consistency of the results between runs with the same K. Each run consisted of 50,000 burn-in iterations and 1,000,000 subsequent MCMC iterations. Because the sampled populations may have had some connection to each other before fragmentation occurred – and may still have – we used the correlated allele frequencies model and the admixture model. We used a separate alpha (degree of admixture) for each population. Alpha varied considerably along the runs when we used the default value of alphapropsd (standard deviation of the normal distribution describing alpha), so we decreased it to 0.005 to derive more accurate estimates of the output parameters (Pritchard et al. 2007).

Inferring gene flow patterns among forest fragments

For all of the following analyses, we removed the birds from sites with small sample sizes (Muñeco and Brasilia had one individual, and Fragment 5 had seven individuals), leaving for analysis 150 birds from six forest fragments.

We first used 2MOD version 0.2 (Ciofi et al. 1999) to test whether the population structure of our sample sites was best reflected by a migration-drift equilibrium model or a drift-only model. This program uses a coalescent-based Monte-Carlo Markov Chain approach to estimate the relative likelihoods of these two models. The gene flow-drift model assumes that allele frequencies in the populations are determined by a balance of genetic drift and immigration. The drift model assumes one panmictic population was fragmented into multiple subpopulations and that subpopulations are diverging in the absence of migration. We performed 5 replicate runs with 500000 iterations each from which we discarded the first 50000 as a burn-in period.

We then employed F-statistics to measure genetic differentiation and index the extent of gene flow among forest fragments. Treating each fragment as a separate population, we calculated pairwise Weir and Cockerham's (1984) θ's among sample sites, and tested these values for significance using GENETIX, set to 10,000 permutations. This form of Fst quantifies the reduction in heterozygosity within populations relative to the total population, assuming that one single population is the ancestor of all other populations. Although F-statistics may be inappropriate for microsatellites because of their high rate of mutation, Weir and Cockerham's (1984) θ is one of the most widely used and conservative approaches to calculating differentiation (Lowe et al. 2004).

We tested for the existence of isolation by distance by testing the correlation between genetic and geographic distances. We performed a Mantel test between Fst/(1-Fst) and the logarithm of the Euclidean geographic distances among fragments (Rousset 1997) using GENEPOP version 3.4 (Raymond and Rousset 1995). We calculated two sets of geographic distance values: the distance between actual netting locations, and the shortest distance between the edges of each pair of fragments. Because we assumed that birds could move freely within a forest fragment, this second type of distance value represents the distance through non-forest habitat that a bird would have to travel through to move between fragments.

Within-population genetic diversity

To test whether there was a reduction of genetic diversity in small forest fragments, we calculated within-population genetic diversity metrics for each forest fragment (except Muñeco, Brasilia, and Fragment 5, because of their small sample sizes) using the program FSTAT version 2.9.3.2 (Goudet 2001) to calculate allelic richness, and GENALEX (Peakall and Smouse 2006) to calculate the number of private alleles. The allelic richness of each locus (corrected for differences in sample size) was summed for each population to derive a total allelic richness per forest fragment. Graphical distributions of the values of allelic richness (R) and observed heterozygosity (H_{obs}) indicated that neither set of values was normally distributed (we did not use a normality test because the sample sizes were too small). Therefore we used a two-tailed Spearman rank correlation test (Siegel 1956) to assess the correlation between both R and fragment size, and between H_{obs} and fragment size.

Results

Microsatellite validation and variability

A total of 159 birds were genotyped at 15 microsatellite loci (Table 5), but two of these loci (CoAl21 and CoAl24) were subsequently removed from analyses due to the possible presence of null alleles in two populations for locus CoAl21 and five populations for locus CoAl24; when all birds were treated as a single population, the estimated frequency of null alleles was 0.0396 for CoAl21 and 0.2243 for CoAl24. All loci were polymorphic, with allele diversities ranging from 5 (CoAl68 and CoAl86) to 23 (CoAl02), and a mean of 10.5 alleles per locus. The global test for Hardy-Weinberg equilibrium indicated no significant heterozygote deficiency (P=0.734) and no significant deficiency/excess of heterozygotes was found for any fragment after FDR correction (Table 5). All Fis values were not significantly

Table 5. Summary of sample sizes and genetic diversity parameters

Site	fragment size (ha)	N[a]	Allelic richness	H_{exp} n.b.[b]	H_{obs}[c]	HW excess/ deficiency p-values[d]	Fis[e]	# private alleles
Altamira	-[f]	14	81.0	0.682	0.659	0.167	0.035	3
Cedeño	15	19	84.0	0.710	0.717	0.680	0.010	2
Fragment 9	20	26	80.9	0.695	0.719	0.167	0.035	1
Guaymi	5600	49	87.5	0.728	0.744	0.167	0.022	9
Loma Linda	35	18	86.7	0.734	0.744	0.464	0.013	3
Sabalito	20	24	81.6	0.706	0.692	0.325	0.020	1

[a] number of manakins genotyped/fragment

[b] expected heterozygosity, corrected for sampling bias

[c] observed heterozygosity

[d] FDR-corrected p-values of the tests of heterozygote excess/deficiency relative to Hardy-Weinberg equilibrium per fragment (the test of excess was performed when Hobs > Hexp n.b., the test of deficiency when Hobs < Hexp n.b.)

[e] all of the Fis values were not significant ($p>0.05$)

[f] the effective fragment size of Altamira is unknown, but it is most likely the largest fragment

different than zero. No pairs of loci showed significant linkage disequilibrium after correction for multiple comparisons.

Population structure

In all 12 GENELAND runs, the modal number of genetic groups estimated along the MCMC was 1. The STRUCTURE analyses similarly indicated that most likely all samples belong to the same genetic group. Indeed, the estimated probability of K=1 genetic group was 1, and this result was confirmed by the plot of the log likelihood values for each value of K, in which the highest likelihood was obtained with K=1 (Fig. 3).

Inferring gene flow patterns among forest fragments

The five runs performed in 2MOD gave similar results, indicating that the MCMCs were long enough to reach convergence. The migration-drift model was much more likely than the pure drift model (P(migration-drift equilibrium) = 0.87, Bayes factor = 6.44).

Pairwise θ values ranged from 0.001 to 0.029 (Table 6). 7 of 15 pairwise comparisons were significant, all of which involved Altamira or Fragment 9. Mantel tests showed no association between genetic distance and either measure of geographic distance ($p = 0.325$ for distance between sample sites, and $p=0.332$ for distance between fragment edges; Fig. 4).

Within-population genetic diversity

Allelic richness, observed heterozygosity, and number of private alleles did not display any clear relationship with fragment area (Table 5). The correlation between allelic richness and fragment size was not significant (Spearman's $R_s = 0.086$, $p>0.1$)

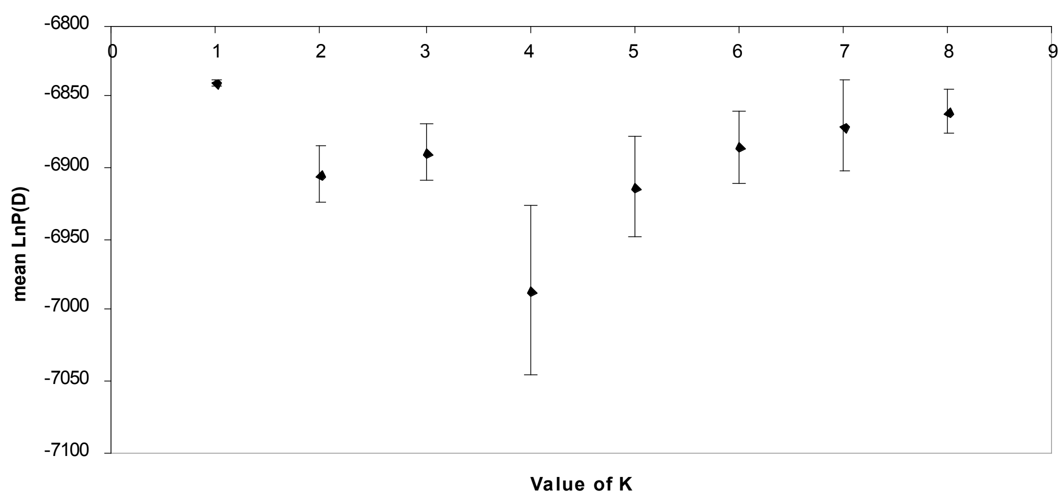

Figure 3. Mean log likelihood scores as a function of the number of genetic groups (K), calculated over the five STRUCTURE runs for each value of K. Error bars indicate one standard deviation. The most likely number of genetically distinct manakin populations is 1.

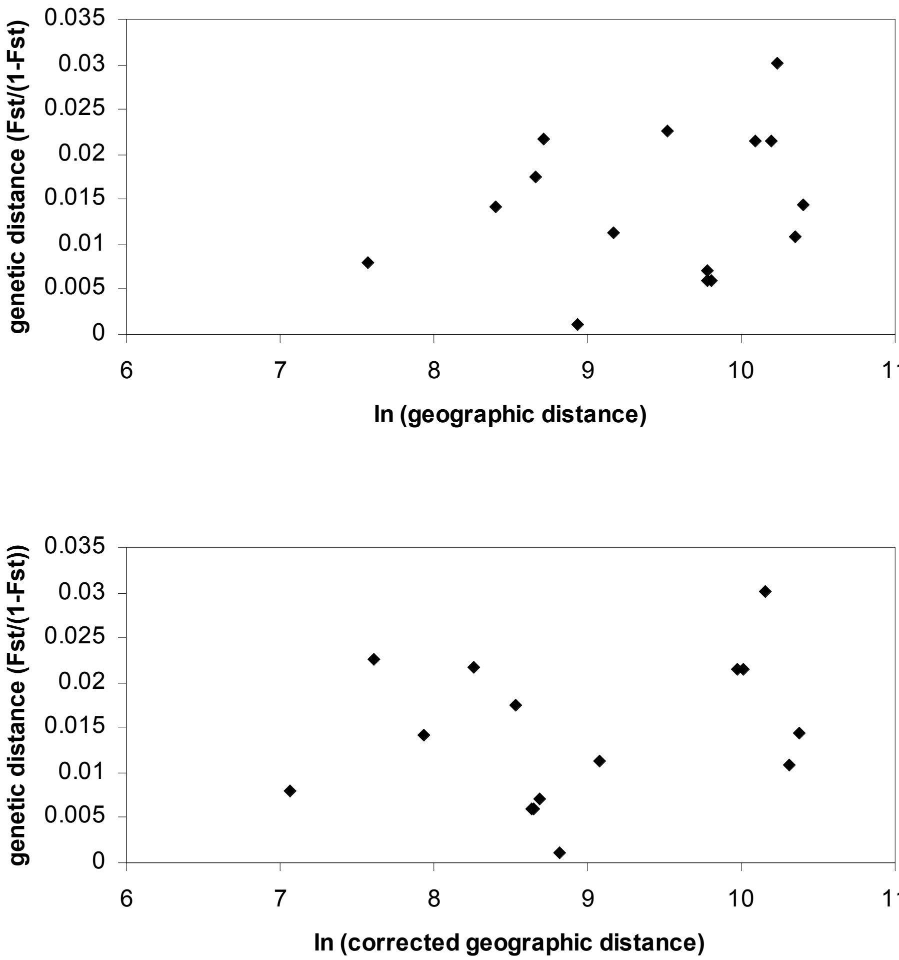

Figure 4. Comparisons of pairwise genetic distances and pairwise geographic distances. "Geographic distance" represents the Euclidean distance between locations where birds were sampled, whereas "corrected geographic distance" represents the distance between the closest edges of the respective forest fragments.

Table 6. Pairwise Weir and Cockerham's θ (upper) and the corresponding FDR-corrected p-values of the permutation tests (lower). Asterisks indicate P-values significant at the 0.05 threshold.

	Altamira	Cedeño	Fragment 9	Guaymi	Loma Linda	Sabalito
Altamira		0.011	0.029	0.021	0.014	0.021
Cedeño	0.08		0.014	0.007	0.008	0.001
Fragment 9	0*	0.01*		0.022	0.017	0.021
Guaymi	0*	0.05	0*		0.006	0.006
Loma Linda	0.06	0.10	0.01*	0.08		0.011
Sabalito	0.01*	0.41	0*	0.06	0.05	

nor was the correlation between observed heterozygosity and fragment size (Spearman's Rs = 0.086, p>0.1). Although the effective size of the Altamira fragment was unknown, it is part of a very large forest and so was given the highest size rank for the correlation analyses. The Guaymi fragment exhibited the highest values for allelic richness, observed heterozygosity, and private alleles, while the Altamira fragment had among the lowest values for these three metrics.

Discussion

A striking result of this study is that despite the highly fragmented habitat mosaic occupied by this forest-dependent bird, we found little evidence for genetic structuring among White-ruffed Manakins distributed among nine isolated forest fragments. Bayesian analyses in both GENELAND and STRUCTURE indicated that all of the sampled birds group into a single genetic population. Although almost half the estimated pairwise Fst values (ranging from 0.014 to 0.029) were significant, all involved two specific fragments (the Altamira fragment or Fragment 9). The other values indicated little to moderate differentiation (Wright, in Hartl and Clark 1989), ranging from 0.001 to 0.014. In the Long-tailed Manakin (*Chiroxiphia linearis*), McDonald (2003) found similarly low differentiation, with an Fst value of 0.02 between 2 populations 115 km apart. In our study there was a lack of strong geographic patterning in the Fst values. The significant differentiation of Altamira from most of the other sites could be explained by the fact that Altamira is the most geographically distant, but the lack of significant differentiation between Altamira and Cedeño and Altramira-Loma Linda is then surprising. There are no obvious landscape characteristics that explain the differentiation of Fragment 9 from all the other fragments since this fragment is relatively close to the Las Cruces Biological Station forest reserve, which would facilitate rather than impede movement. The observed differentiation could be due to the fact that the fragments were formerly part of a continuous population and were recently isolated, triggering differentiation among some of them, by chance, through the effects of drift. However, this hypothesis can be excluded since 2MOD suggested that the studied sites are at migration-drift equilibrium and not under the effect of drift alone.

Even though some of the fragments appeared to be significantly genetically differentiated, there was no statistical evidence for a deviation from Hardy-Weinberg equilibrium. This is peculiar, as one would expect a significant deficiency of heterozygotes in the whole sample, as a result of a Wahlund effect. One possible explanation could be that the Wahlund effect is too weak to affect Hardy-Weinberg equilibrium, as only two fragments (Altamira and Fragment 9) are significantly differentiated from some of the others, and the Bayesian clustering methods did not find any genetic structure in the data set. Including only the individuals from Altamira and Fragment 9, there was still no significant deviation from HWE.

Perhaps even more surprising than the weak genetic structuring, within-population genetic diversity appeared to be unaffected by habitat fragmentation, as allelic diversity and observed heterozygosity showed no significant relationship with forest fragment size. Contrary to our expectations, our site located in the largest forest fragment (Altamira) showed comparatively low values for both allelic richness and heterozygosity. Although this site is situated on the periphery of a large forest reserve (500,000 ha), it is uncertain what proportion the total habitat falls within the distributional range of this species, since much of the reserve contains mountains that are higher than the elevational range of this manakin.

These analyses of both genetic differentiation and genetic variation suggest that habitat fragmentation has not resulted in strong genetic effects on populations of White-ruffed Manakins at the relatively fine spatial and short temporal scales of this study system. This finding of low genetic structure is interesting in broader ecological and conservation contexts, because forest-dependent tropical birds are typically considered to be highly sensitive to movement limitation due to habitat fragmentation (Laurance et al. 2004).

The absence of strong genetic effects on the study population may have three causes, which we discuss below.

First, recent fragmentation may have indeed affected the dispersal patterns of this species, but there simply has not been enough time since fragmentation of the landscape began for genetic differences to accumulate. Historical aerial photographs of the region show that some deforestation had occurred by 1960, and deforestation comparable to that of the present day had been reached by the 1970s. Assuming that the 1960 level of deforestation was enough to impede dispersal, this leaves at most half a century for limited dispersal to result in genetic differentiation among fragments. Even this maximum time frame for the accumulation of genetic differences is relatively short in terms of the probable generation time for these manakins: although difficult to estimate for this system, the average parental age at which successful offspring are produced is at least 3-4 years, and probably much longer for males than females (Rosselli 2002). However, 2MOD suggests that the study area is more likely to be at migration-drift equilibrium than under drift alone, indicating that the gene flow pattern is unlikely to have been greatly modified by fragmentation.

Another possibility is that the limited genetic effects stem from markers of insufficient power, limited spatial scale, or small sample sizes. It seems unlikely that we would be unable to detect robust patterns of spatial genetic structuring, as studies have used as few as six microsatellite markers to reveal fine-scale genetic structure and estimate dispersal in birds with mating clusters such as leks (Hoglund and Shorey

2003) or cooperatively breeding groups (Woxvold et al. 2006) at similar spatial scales. Thus, the low differentiation we found in the White-ruffed Manakins across this landscape is likely not due to a gross lack of sensitivity in the molecular markers. On the other hand, a spatial scale of tens of kilometers may be too small to accumulate differentiation in a species as mobile as the White-ruffed Manakin, as a study of the Long-tailed Manakin similarly found little differentiation between sites separated by 115 km (McDonald 2003), although only four microsatellite loci were used in that study. Sample size effects may be more of an issue in the comparisons of fragment size with allelic diversities, but we note that the variation in allelic richness and related metrics was low across fragment sizes that, in contrast, varied by several orders-of-magnitude.

Last, this species may maintain high levels of dispersal potential and population connectivity despite the fragmentation of its forest habitat, as has been shown for the White-starred Robin in Kenya (Galbusera et al. 2004). As mentioned earlier, this hypothesis is supported by the results of the analyzes we performed with 2MOD, which showed that in the study area the species was likely to be at migration-drift equilibrium. Hence the recent fragmentation of the landscape would not have affected the gene flow and movement capacities of the White-ruffed Manakin in our study area. This confirms observations that suggest a high movement potential for this species: whereas understory insectivores are the category of Neotropical birds most often identified as vulnerable to possible dispersal limitation due to fragmentation, the ecology and movement abilities of the frugivorous White-ruffed Manakin suggested that this species may be able to maintain some inter-fragment connectivity in a habitat mosaic. Behavioral observations indicate that although these manakins typically occupy interior forest habitat, individuals do venture into clearings and more open edge habitats in search of fruits, which comprise the majority of their diet (Skutch

1967; Rosselli 1994). In general, frugivorous species tend to forage more widely than insectivores in search of food, and thus may have greater movement capacities. Furthermore, male and female manakins do not differ in capture probabilities in both continuous and fragmented landscapes, indicating that individuals likely move over great distances to find scattered fruit resources (Blake and Loiselle 2002; Ruiz-Gutierrez et al. *in press*). The White-ruffed Manakin, therefore, might be expected to have a higher dispersal capacity than the more understory-dependent, insectivorous species that have been identified as particularly sensitive to habitat fragmentation (Stouffer and Bierregaard 1995; Canaday 1996; Anciaes and Marini 2000; Brown et al. 2004). Relative to other frugivorous manakins, White-ruffed Manakins may have stronger movement capacities as suggested by observations that this species tends to frequent the higher strata of the forest when other more understory-dependent manakins are present (Skutch 1967). White-ruffed Manakins on the Atlantic slope of Costa Rica are also suspected of undertaking seasonal altitudinal movements through forest habitat to lower elevations in the non-breeding season (Skutch 1967; Rosselli 1994; Blake and Loiselle 2002), indicating that individuals might be capable of regularly moving across large distances. Individuals have also been captured and observed flying through non-forested habitats such as coffee and pasture) (Ruiz-Gutierrez unpublished data). This species may thus possess sufficient movement capabilities to maintain high rates of migration among isolated forest remnants. Before this study it was unclear whether these movement capacities translate into successful dispersal and reproduction, but the genetic evidence presented here indicates ongoing gene flow across this fragmented landscape.

The White-ruffed Manakins in this study area are unlikely to face immediate genetic threats stemming from the recent fragmentation of their preferred forest habitat. Demographic processes relevant to manakin conservation likely operate at broader regional scales, as local manakin populations have usually not been considered particularly sensitive to habitat fragmentation (Anciaes and Marini 2000; Uezu et al. 2005; Anciaes and Peterson 2006). Keeping in mind that different species are affected by habitat fragmentation in disparate ways (e.g. Anciaes and Marini 2000; Galbusera et al. 2004; Uezu et al. 2005), this study highlights the importance of considering species characteristics along with the appropriate spatial and temporal scales in any assessment of the genetic effects of habitat fragmentation.

REFERENCES

American Ornithologists' Union (1983) Check-list of North American Birds, 7th edition (1998), Washington, DC

Anciaes M, Marini MA (2000) The effects of fragmentation on fluctuating asymmetry in passerine birds of Brazilian tropical forests. J Appl Ecol 37:1013-1028

Anciaes M, Peterson AT (2006) Climate change effects on Neotropical manakin diversity based on ecological niche modeling. Condor 108:778-791

Barnett JR, Stenzler LM, Ruiz-Gutierrez V, Bogdanowicz SM, Lovette IJ (2007) Isolation and characterization of microsatellite markers from the White-ruffed Manakin, *Corapipo altera* (Aves, Pipridae). Mol Ecol Notes (in press)

Bates JM (2000) Allozymic genetic structure and natural habitat fragmentation: Data for five species of Amazonian forest birds. Condor 102:770-783

Bates JM (2002) The genetic effects of forest fragmentation on five species of Amazonian birds. J Avian Biol 33:276-294

Belkhir K, Borsa P, Chikhi L, Raufaste N, Bonhomme F (1996-2004) GENETIX 4.05, logiciel sous Windows TM pour la génétique des populations. Laboratoire Génome, Populations, Interactions, CNRS UMR 5000, Université de Montpellier II, Montpellier (France)

Benjamini Y, Hochberg Y (1995) Controlling the False Discovery Rate - a Practical and Powerful Approach to Multiple Testing. J Royal Statistical Society Series B-Methodological 57:289-300

Blake JG, Loiselle BA (2002) Manakins (Pipridae) in second-growth and old-growth forest: patterns of habitat use, movement, and survival. Auk 119:132–148

Borgella R, Snow AA, Gavin TA (2001) Species richness and pollen loads of hummingbirds using forest fragments in southern Costa Rica. Biotropica 33:90-109

Borgella R, Gavin TA (2005) Avian community dynamics in a fragmented tropical landscape. Ecol Appl 15:1062-1073

Brown LM, Ramey RR II, Tamburini B, Gavin TA (2004) Population structure and mitochondrial DNA variation in sedentary Neotropical birds isolated by forest fragmentation. Conserv Genet 5:743-757

Brownstein MJ, Carpten JD, Smith JR (1996) Modulation of non-templated nucleotide addition by Taq DNA polymerase: primer modifications that facilitate genotyping. Biotechniques 20:1004-1010

Brumfield RT, Capparella AP (1996) Historical diversification of birds in northwestern South America: A molecular perspective on the role of vicariant events. Evolution 50:1607-1624

Caizergues A, Ratti O, Helle P, Rotelli L, Ellison L, Rasplus J (2003) Population genetic structure of male black grouse (Tetrao tetrix L.) in fragmented vs. continuous landscapes. Mol Ecol 12:2297-2305

Canaday C (1996) Loss of insectivorous birds along a gradient of human impact in Amazonia. Biol Conserv 77:63-77

Capparella AP (1988) Genetic variation in neotropical birds: Implications for the speciation process. Proceedings of the International Ornithological Congress 19:1658-1664

Capparella AP (1992) Neotropical avian diversity and riverine barriers. Proceedings of the International Ornithological Congress 20:307-316

Castellon TD, Sieving KE (2006) An experimental test of matrix permeability and corridor use by an endemic understory bird. Conserv Biol 20:135-145

Ciofi C, Beaumont MA, Swingland IR, Bruford MW (1999) Genetic divergence and units for conservation in the Komodo Dragon Varanus. P Roy Soc B-Biol Sci 266: 2269-2274

Doherty PF, Grubb TC (2002) Survivorship of permanent-resident birds in a fragmented forested landscape. Ecology 83:844-857

Falush D, Stephens M, Pritchard JK (2003) Inference of population structure using multilocus genotype data: linked loci and correlated allele frequencies. Genetics 164:1567-1587

Ferraz G, Nichols JD, Hines JE, Stouffer PC, Bierregaard RO, Lovejoy TE (2007) A large-scale deforestation experiment: effects of patch area and isolation on Amazon birds. Science 315:238-241

Francisco MR, Galetti PM, Gibbs HL (2004) Isolation and characterization of microsatellite loci in the blue manakin, Chiroxiphia caudata (Aves, Pipridae). Mol Ecol Notes 4:758-760

Frankham R (1996) Relationship of genetic variation to population size in wildlife. Conserv Biol 10:1500-1508

Galbusera P, Githiru M, Lens L, Matthysen E (2004) Genetic equilibrium despite habitat fragmentation in an Afrotropical bird. Mol Ecol 13:1409-1421

Goudet J (2001) FSTAT, a Program to Estimate and Test Gene Diversities and Fixation Indices Version 2.9.3.2. Available from http://www2.unil.ch/popgen/softwares/fstat.htm. Cited Mar 2007

Guillot G, Estoup A, Mortier F, Cosson JF (2005a) A spatial statistical model for landscape genetics. Genetics 170:1261-1280

Guillot G, Mortier F, Estoup A (2005b) Geneland: a program for landscape genetics. Mol Ecol Notes 5:712-715

Hailer F, Gautschi B, Helander B (2005) Development and multiplex PCR amplification of novel microsatellite markers in the White-tailed Sea Eagle, Haliaeetus albicilla (Aves: Falconiformes, Accipitridae). Mol Ecol Notes 5:938-940

Hartl DL, Clark AG (1989) Principles of Population Genetics. 2 ed. Sinauer Associates, Sunderland, Massachusetts. 682 pp.

Hoglund J, Shorey L (2003) Local genetic structure in a white-bearded manakin population. Mol Ecol 12:2457-2463

Ihaka R, Gentleman R (1996) R. A language for data analysis and graphics. J Comput Graph Stat 5:299-314

Karr JR, Freemark KE (1983) Habitat selection and environmental gradients - dynamics in the stable tropics. Ecology 64:1481-1494

Kattan GH, Alvarez-Lopez H, Giraldo M (1994) Forest fragmentation and bird extinctions – San-Antonio 80 years later. Conserv Biol 8:138-146

Koenig WD, Van Vuren D, Hooge PN (1996) Detectability, philopatry, and the distribution of dispersal distances in vertebrates. Trends Ecol Evol 11:514-517

Laurance WF, Lovejoy TE, et al. (2002) Ecosystem decay of Amazonian forest fragments: A 22-year investigation. Conserv Biol 16:605-618

Laurance SGW, Stouffer PC, Laurance WF (2004) Effects of road clearings on movement patterns of understory rainforest birds in central Amazonia. Conserv Biol 18:1099-1109

Laurance SGW, Gomez MS (2005) Clearing width and movements of understory rainforest birds. Biotropica 37:149-152

Lowe A, Harris S, Ashton P (2004) Ecological Genetics: Design, Analysis, and Application. Blackwell, Oxford, UK

McDonald DB (2003) Microsatellite DNA evidence for gene flow in neotropical lek-mating long-tailed manakins. Condor 105:580-586

Peakall R, Smouse PE (2006) GENALEX 6: genetic analysis in Excel. Population genetic software for teaching and research. Mol Ecol Notes 6:288-295

Pritchard JK, Stephens M, Donnelly P (2000) Inference of population structure using mutilocus genotype data. Genetics 155:945-959

Pritchard JK, Wen X, Falush D (2007) Documentation for structure software: version 2.2. http://pritch.bsd.uchicago.edu/software/structure22/readme.pdf. Cited Mar 2007

Raymond M, Rousset F (1995) GENEPOP version 1.2: population genetics sofware for exact tests and ecuminicism. J Hered 86:248-249

Renjifo LM (1999) Composition changes in a subandean avifauna after long-term forest fragmentation. Conserv Biol 13:1124-1139

Ricklefs RE, Bermingham E (2001) Nonequilibrium diversity dynamics of the Lesser Antillean avifauna. Science 294:1522-1524

Robinson SK, Thompson FR, Donovan TM, Whitehead DR, Faaborg J (1995) Regional forest fragmentation and the nesting success of migratory birds. Science 267:1987-1990

Robinson WD (1999) Long-term changes in the avifauna of Barro Colorado Island, Panama, a tropical forest isolate. Conserv Biol 13:85-97

Robinson WD, Robinson TR, Robinson SK, Brawn JD (2000) Nesting success of understory forest birds in central Panama. J Avian Biol 31:151-164

Rosselli L (1994) The annual cycle of a tropical frugivorous altitudinal migrant *Corapipo leucorrhoa* (Pipridae) and its fruit resources. Bird Conserv Int 4:143-160

Rosselli L, Vasquez P, Ayub I (2002) The courtship displays and social system of the white-ruffed manakin in Costa Rica. Wilson Bull 114:165-178

Rousset F (1997) Genetic differentiation and estimation of gene flow from F-statistics under isolation by distance. Genetics 145:1219-1228

Ruiz-Gutierrez V, Gavin TA, Dhondt AA. (*in press*) Effects of forest fragmentation on the survival of White-ruffed manakins in southwestern Costa Rica. Ecological Applications.

Sala O, Chapin F, Armesto J, Berlow E, Bloomfield J, Dirzo R, Huber-Sanwald E, Huenneke L, Jackson R, Kinzig A, Leemans R, Lodge D, Mooney H, Oesterheld M, Poff N, Sykes M, Walker B, Walker M, Wall D (2000) Biodiversity - Global biodiversity scenarios for the year 2100. Science 287:1770-1774

Siegel S (1956) Nonparametric statistics for the behavioral sciences. McGraw-Hill, Tokyo

Sieving KE (1992) Nest predation and insular extinction of selected forest birds on Barro Colorado Island, Panama. Ecology 73:2310-2328

Skutch AF (1967) Life histories of Central American highland birds: White-ruffed Manakin (*Corapipo leucorrhoa*). Pub Nuttall Orn Club 7:68-75

Slud P (1964) Birds of Costa Rica. B Am Mus Nat Hist 128:237-238

Stouffer PC, Bierregaard RO (1995) Use of amazonian forest fragments by understory insectivorous birds. Ecology 76:2429-2445

Stouffer PC, Bierregaard RO, Strong C, Lovejoy TE (2006) Long-term landscape change and bird abundance in Amazonian rainforest fragments. Conserv Biol 20:1212-1223

Stratford JA, Stouffer PC (1999) Local extinctions of terrestrial insectivorous birds in a fragmented landscape near Manaus, Brazil. Conserv Biol 13:1416-1423

Thery, M (1992) The evolution of leks through female choice: differential clustering and space utilization in six sympatric manakins. Behav Ecol Sociobiol 30:227-237

Uezu A, Metzger JP, Vielliard JME (2005) Effects of structural and functional connectivity and patch size on the abundance of seven Atlantic Forest bird species. Biol Conserv 123:507-519

Van Oosterhout C, Hutchinson WF, Wills DPM, Shipley P (2004) MICRO-CHECKER: software for identifying and correcting genotyping errors in microsatellite data. Mol Ecol 4:535-538

Weir BS, Cockerham CC (1984) Estimating F-statistics for the analysis of population structure. Evolution 38:1358–1370

Wilson GA, Rannala B (2003) Bayesian inference of recent migration rates using multilocus genotypes. Genetics 163:1177-1191

Woxvold IA, Adcock GJ, Mulder RA (2006) Fine-scale genetic structure and dispersal in cooperatively breeding apostlebirds. Mol Ecol 15:3139-3146

Zanette LP, Doyle P, Tremont SM (2000) Food shortage in small fragments: Evidence from an area-sensitive passerine. Ecology 81:1654-1666

CHAPTER 4

OCCUPANCY DYNAMICS IN A TROPICAL BIRD COMMUNITY: FOREST USE IS FAVORED ACROSS SPECIES

Abstract

Worldwide loss of biodiversity necessitates a clear understanding of the factors driving population declines as well as informed predictions about which species and populations are at greatest risk. For most populations, the biggest threats to their long-term persistence are the reduction and changes in configuration of their natural habitat. There have been noted inconsistencies in responses of populations across landscapes to habitat loss and fragmentation, widely attributed to the effects of the matrix habitats in which focal habitat fragments are typically embedded. We broadly quantified potential effects of the inter-patch matrix by estimating occupancy and colonization of forest and surrounding non-forest matrix by using a dynamic multi-species hierarchical model on a diverse community of birds in southwestern Costa Rica. We found higher levels of occupancy and colonization of forest across species in comparison to the non-forest matrix. Species' prior ecological classification of forest dependency was a poor predictor of overall occupancy dynamics of both habitat types. Synthesis and applications: We identified 39 species of conservation concern, defined by having high estimates of occupancy of forest, and low estimates of occupancy and colonization of non-forest, and thus most likely to be vulnerable to the effects of habitat loss and fragmentation. We propose the use of the presented hierarchical community model to estimate occupancy dynamics of focal and inter-patch matrix habitats to identify which species in a community, specific to a region of interest, are likely to be most vulnerable to the effects of habitat loss and fragmentation.

Introduction

Determining how animal populations relate to their environment is the fundamental basis for understanding how population processes are affected by changes in landscape characteristics (Kareiva & Wennergren, 1995). Current declines in biodiversity, widely attributed to habitat loss and fragmentation, have motivated ecologists to improve predictions regarding the responses of wildlife populations to changes in the amounts and configurations of available habitat (Wiens, 1996; Balmford, Green & Jenkins, 2003). This work requires identification of key environmental features that are directly linked to species' long-term probabilities of persistence in a landscape after a fragmentation event. Original research on this topic grew from metapopulation theory (Levins, 1969) and island biogeography theory (MacArthur and Wilson, 1967), to metapopulation biology and landscape ecology, establishing a broad base of knowledge on how landscape characteristics could drive the dynamics of species' distributions (Haila, 2002; Laurance, 2008). This work spans several decades of research, mainly focused on how the long-term persistence of a species in a given habitat patch is related to patch size and isolation (Andrén, 1994; Hanski, 1999; Driscoll, 2007).

Despite available knowledge, there is no clear consensus on the roles that patch size and isolation play on the distribution of species in fragmented landscapes (Bender, Contreras & Fahrig, 1998; Debinski & Holt, 2000; Ewers & Didham, 2006). A plausible explanation might be that the distribution of most species in fragmented landscapes does not reflect the assumed "island system" in metapopulation biology, where the landscape is divided into occupied habitat patches and un-occupied surrounding matrix (Moilanen, 2002). This idea is supported by findings from a recent meta-analysis, using multiple taxa across different continents, which concluded that patch size and isolation are "poor predictors" of which species are likely to persist in a habitat patch (Prugh *et al.*, 2008). Prugh *et. al* (2009) tested several plausible reasons for inconsistent predictive abilities of patch-related measures, of which the composition of the inter-patch habitat matrix was found to be the strongest predictor of species sensitivity to patch size and isolation. These results are consistent with mounting theoretical and empirical evidence suggesting that a significant number of species in heterogeneous landscapes might be able to use, occupy, and even persist in the inter-patch habitat matrix (Vandermeer & Carvajal, 2001; Bender & Fahrig, 2005; Driscoll, 2005; Debinski, 2006; Revilla & Wiegand, 2008). However, most research on "matrix" effects has focused on species richness, or the presence or absence of a single or a subset of "habitat specialist" species, for both focal and matrix habitats (*i.e.* Wethered & Lawes, 2003; Antongiovanni & Metzger, 2005).

To build upon our current understanding on how populations respond to changes in their environment, it is necessary to estimate how species occupy both focal and surrounding matrix habitats. Improved research on this topic is highly relevant to conservation science and wildlife management (Blaum & Wichmann, 2007; Franklin & Lindenmayer, 2009), especially for regions where it is more feasible to improve the quality of the matrix than increase the proportion of focal habitat (Rudel, 2006; Perfecto & Vandermeer, 2008).

The impact of changes in the amount and configuration of available habitat are traditionally modeled by examining the probability that a habitat patch is occupied using two main approaches: the colonization-extinction (CE) approach widely used in metapopulation biology (Hanski, 1992; 1999), and the birth-immigration-death-emigration (BIDE) approach mainly applied in landscape ecology (Fahrig, 2002). For the CE model, patch occupancy is dependent on colonization and extinction dynamics. As habitat area decreases, colonization of unoccupied habitat patches decreases, and assumed to be a function of the size and number of near-by occupied patches (Hanski, 1999). Individuals are also assumed to occupy only focal habitat patches, and merely disperse through the matrix. Recent work on matrix effects under the CE framework has modeled incorporated ease of movement through different matrix types (Hein et al., 2004; Ovaskainen, 2004). In contrast, the BIDE model predicts that as habitat area deceases, colonization of the matrix increases, where mortality is assumed to be higher (Fahrig, 2002). The result is an overall reduction in population size, decreasing immigration into, and increasing emigration rates out of habitat patches (Fahrig, 2002). Although the BIDE framework addresses matrix effects, similarly to the CE approach, it has yet to jointly incorporate occupancy dynamics of both focal and matrix habitats into their approach.

These approaches are currently applied to make general predictions regarding the probability that a sample unit (patch) is occupied by an individual or species (i.e. the state variable of occupancy) and related dynamics: colonization (i.e. probability that a sample unit is occupied given it was unoccupied the previous sampling period) and extinction (the probability that a sample unit is unoccupied given that it was occupied the previous sampling period) (Hanski, 1992; MacKenzie et al., 2006). However, most of the predictions based on occupancy dynamics in fragmented landscapes under the CE and BIDE models largely assume that an animal was absent when not observed in a habitat patch (Moilanen, 2002; MacKenzie, 2006). There is irrefutable evidence that the detectability of most animals is less than perfect and can vary by habitat type, suggesting that individuals or species could be present in a habitat patch, but not detected (Williams, Nichols & Conroy, 2002; Mackenzie & Royle, 2005). Current methodology in occupancy dynamics modeling accounts for the likelihood of these false absences, generating more accurate predictions with regards to the true state of occupancy and related dynamics (Royle & Link, 2006; Nichols et al., 2008). This separation of true occupancy from apparent absences is specifically important in making predictions on patch and matrix occupancy dynamics; differences in occupancy rates between focal habitat patches and surrounding matrix could be masked or biased by potentially different rates in detectability (Boulinier et al., 1998; Moilanen, 2002; Driscoll, 2007). There are notable examples of work on occupancy dynamics that account for detectability (*i. e.* Boulinier at al., 2001; Hames et al, 2001; Ferraz et al., 2007; Radford & Bennett, 2007; Francois, Alexandre & Julliard, 2008) but they only address potential matrix effects and do not specifically contrast occupancy dynamics between habitat types.

In this paper, we estimated potential differences in species' use of both focal and matrix habitat types by estimating probabilities of occupancy and colonization of forest and intervening non-forest matrix habitats, for a community of bird species in southwestern Costa Rica. We developed a multi-species hierarchical community model that estimates species-specific occupancy and colonization and detection, thus accounting for potential differences in detectability between species and habitat types. By analyzing species using a hierarchical approach, we gained additional insight into the validity of ecological classifications widely used in occupancy studies, by testing *a priori* expectations on how occupancy and colonization of forest and non-forest habitats should vary among pre-determined categories of forest dependency across species (Stiles, 1985). The analytical model and framework presented here can be applied under both CE and BIDE approaches to make more accurate predictions with regards to environmental factors driving occupancy dynamics of populations in fragmented landscapes, as well as what species or individuals are most likely to be negatively affected in a given region.

Materials and Methods

Study site and bird surveys

The survey sites are situated within a 7 km radius of the Las Cruces Biological Station of the Organization for Tropical Studies in Coto Brus, southwestern Costa Rica. This once continuous forested region became heavily fragmented in the 1940s and 1950s as forests were cleared to make way for small-scale agriculture. The remnant forest fragments in this region are classified as mid-elevation tropical forests (Borgella & Gavin, 2005). We surveyed 21 point count stations within seven forest (F) fragments ranging in size from 1.4 to 25-ha and situated between 900 and 1,300 m in elevation. We also surveyed 10 point count stations in non-forest matrix (NF) habitat comprised of parcels of pasture, coffee, and secondary growth, also of varying sizes. Point count surveys consisted of recording all birds seen and/or heard in 10 min within 50 mts maximum detection distance. All surveys were conducted from sunrise (~ 5:30 am) until 9:00 am, by the same observer each time. Each point count station was visited three consecutive days each year, rotating the order in which they were visited, during the months of May – September, from 2004 to 2008, although not all points were surveyed the same number of occasions. These months fall within the time of year that most species in the region are known to reproduce (Stiles & Skutch, 1989), reducing the amount of variability in occupancy due to variation in scale of habitat use. Within a given year, we assumed that the populations were closed over the survey period, implying that species were either present or absent for the duration of the three day survey.

Classification of forest dependency

Our categorization of forest dependency for each species was taken from the system developed by Stiles (1985), based on decades of natural history observations and research on the birds of Costa Rica. Species in the "HIGH FD" category are classified as highly forest dependent, and considered as "specialized" and mainly restricted to forest habitats. Species in the "MED FD" category have a moderate degree of forest dependency, and are thought to use both forest and open habitats. Species in the "LOW FD" have a low degree of forest dependency and are associated with open, deforested areas and agricultural habitats (Stiles, 1985).

Analysis

We used a recently developed hierarchical modeling approach that estimates composite community level attributes through species-specific estimates of occupancy, detection, and colonization (Dorazio & Royle, 2005a; Dorazio et al., 2006; Royle and Dorazio, 2008: chapter 12). Under this framework, occurrence models for all individual species are linked together in a multi-level, or hierarchical model, placing then in a context of related community-level responses to environmental factors (Link & Sauer, 2002; Dorazio et al., 2006; Kéry & Royle, 2008). By sharing information across species, we are able to enhance understanding of the community by increasing precision in estimates of species-specific occupancy, detection, and related dynamics, especially for infrequently observed species for which estimates would otherwise be unattainable through individual species analyses (Zipkin et al. In review).

Model

We developed a multi-species hierarchical community model based on survey-specific detection/non-detection records to estimate occupancy dynamics of bird species in forest vs. non-forest habitats. The observations, x(i,j,t,k), denote detection (x=1) or non-detection (x=0) of species *i* (1,2,…,212) at site *j* (1,2,...,31) in year *t* (1,2,..,5) during sampling occasion *k* (1,2,3). We formulated our model by first assuming that occupancy and colonization were species-specific processes that were dependent on habitat type (i.e., forest vs. non-forest). As in previous applications of this method (Kéry & Royle, 2008) we assumed that occupancy for species *i* at site *j* in year *t*, denoted *z* (*i,j,t*), was a latent variable (i.e., imperfectly observed) such that $z(i,j,t)=1$ when species i was present and zero otherwise. If a species in a given location and year was detected, then it could be established that the species was in fact present. However, if a species was not observed, it could be because either the species was present and went undetected or the species was truly absent (MacKenzie & Kendall, 2002). Thus, our repeated sampling protocol ($k > 1$) was designed explicitly to differentiate non-detection from true absences.

We tested for differences in occupancy, colonization and detectability between forest and non-forest habitats by including habitat type (hab) as a binary covariate dependent on whether the sampled site (*j*) was in forest (hab=1) or non-forest (hab=0). The topography in this pre-montane region of Costa Rica is highly variable, with many species showing both upper and lower distributional limits along the elevational continuum. In regions with similar topography and species distributions along elevational gradients, elevation has been successfully applied as a surrogate for key habitat variables that influence distribution and abundance (Kéry & Royle, 2009). We included linear and quadratic elevational covariates in our occupancy model which allowed us to examine species elevational preferences.

We specified the species-specific occurrence model bv assuming that occupancy was a Bernoulli random variable $z(i,j,t) \quad Bern\left(\psi_{i,j,t}\right)$, with probability $\psi_{i,j,t}$ for species *i* in site *j*, during year *t*. For the first year of sampling (t=1), we assumed that species specific occupancy probabilities were linearly related to the above-mentioned habitat covariates, forest type and elevation, on the logit scale (Kéry & Royle, 2009; Russell et al. In press):

$$\text{logit}\left(\psi_{i,j,1}\right) = u1_i hab_j + u2_i\left(1 - hab_j\right) + \alpha 1_i \text{elev}_j + \alpha 2_i \text{elev}_j^2$$

where hab=1 if site j is in a forest and hab=0 otherwise, thus allowing for species-specific occupancy to vary by habitat type. We standardized elevation covariates so that mean elevation was zero. Under this model, $u1_i$ is the probability of occupancy for species i in forested sites under "average" elevation, and likewise, $u2_i$ is the occupancy probability in non-forest sites. The coefficients $\alpha1_i$ and $\alpha2_i$ are the linear and squared effects of elevation on species i, respectively. For t=2,…5, we modified the occupancy model, such that the probability of occupancy for species i in site j was also dependent upon whether or not that species was present in the previous year (Russell et al. In press):

$$\text{logit}\left(\psi_{i,j,t\geq 2}\right) = u1_i z_{j,i,t-1} hab_j + u2_i z_{j,i,t-1}\left(1 - hab_j\right) + w1_i\left(1 - z_{j,i,t-1}\right)hab_j$$
$$+ w2_i\left(1 - z_{j,i,t-1}\right)\left(1 - hab_j\right) + \alpha 1_i \text{elev}_j + \alpha 2_i \text{elev}_j^2$$

Thus $w1_i$ and $w2_i$ are the occupancy probabilities (on the logit scale) for species i in forest and non-forest, respectively, when it was not present in the previous year ($z_{j,i,t-1} = 0$). When a species was in fact present in the previous year ($z_{j,i,t-1} = 1$) then the probability of occupancy simplifies to the original model for the first year of sampling. We thus define the probability of occupancy (expit($\mu1_i$) and expit($\mu2_i$)) as a combination of initial occupancy (the probability that species i was present at site j in the first year of sampling), and continued occupancy (the probability that species i was present at site j given it was present the previous year). The probability of colonization (expit($w1_i$) and expit($w2_i$)) is defined as "the probability that species i was present at site j in year t, given that it was absent at site j in year t-1."

The detection model was similarly assumed to be a Bernoulli random variable, $x(i,j,t,k) \sim Bern\left(\theta_{i,j,t,k} \cdot z(i,j,t)\right)$, where $\theta_{i,j,t,k}$ is the detection probability of species i for the k^{th} sampling period in year t at site j, given that species i was in fact present at site j. When species i was not present, detection was a fixed zero since z

(i,j,t) =0. We assumed that species identity and the habitat type (forest or non-forest) were the only effects on detection:

$\text{logit}\left(\theta_{i,j,t,k}\right) = v1_i hab_j + v2_i\left(1 - hab_j\right).$

In the community hierarchal level of the model, the species-specific parameters were linked together through a common distribution (Royle and Dorazio, 2008). To test the *a priori* hypotheses that species estimates of occupancy, colonization and detection were associated with their prior categorization of forest dependency, we assumed that species parameter estimates (i.e., occupancy, colonization, and detection) were related only to other species within their category and also stratified by habitat type. For example, all species in the HIGH FD category were linked together by assuming that their parameter values for occupancy (and similarly for colonization and detection) were drawn from a common distribution dependent on habitat type. Specifically, we assumed that $u1_{i \in high} \sim N\left(\mu_{u1\_high}, \sigma_{u1\_high}\right)$ where μ_{u1_high} is mean occupancy across the HIGH FD species in forests and σ_{u1_high} is the standard deviation (among HIGH FD species in forests) and that $u2_{i \in high} \sim N\left(\mu_{u2\_high}, \sigma_{u2\_high}\right)$ is the distribution for HIGH FD species in non-forest sites. We similarly defined the hyper-parameters (i.e. the mean and standard deviations – across species in a given group – of occupancy, colonization, and detection) for MED FD and LOW FD species groups. We assumed that species-specific elevation effects were related across all species (independent of forest dependency classification) and accordingly defined common distributions for the linear and squared effects, respectively.

Model specifications and implementation details are provided in Appendix A.

Predictions based on prior ecological classification

We predicted that occupancy and colonization in forest across HIGH FD species would be higher than MED FD species, followed by LOW FD species (i.e. $\mu_{u1\_high} > \mu_{u1\_med} > \mu_{u1\_low}$). We expected the opposite pattern for non-forest habitats, with occupancy and colonization for LOW FD species with the highest values, followed by MED FD species, and HIGH FD species showing the lowest mean response (i.e. $\mu_{\mu2\_high} < \mu_{\mu2\_med} < \mu_{\mu2\_low}$).

Results

Avian community

We observed 212 diurnal species in 31 sites on at least one occasion over the five years of sampling. We did not have sufficient data to estimate occupancy, colonization, and detection for 139 of the 212 species (i.e., rare species would result in unsubstantiated parameter estimates). Even though we were unable to obtain information about a large proportion of the observed species, our hierarchical community model was able to produce parameter estimates for many more species than if we had modeled each species separately (Zipkin et al, In review). However, since we focused on a subset of the most frequently observed species, estimates of occupancy were fairly high overall and are likely not indicative of the excluded species. Posterior summaries of species-specific model parameters for occupancy are presented in Appendix B, for colonization in Appendix C, and detection in Appendix D.

Occupancy of forest vs. non-forest

The posterior distributions of mean occupancy for HIGH (n=13), MED (n=39), and LOW FD (n=21) species indicated that all groups had fairly high and similar occupancy in forest habitats (Fig 5a. with $\mu_{u1\_high} \sim \mu_{u1\_med} \sim \mu_{u1\_low}$).

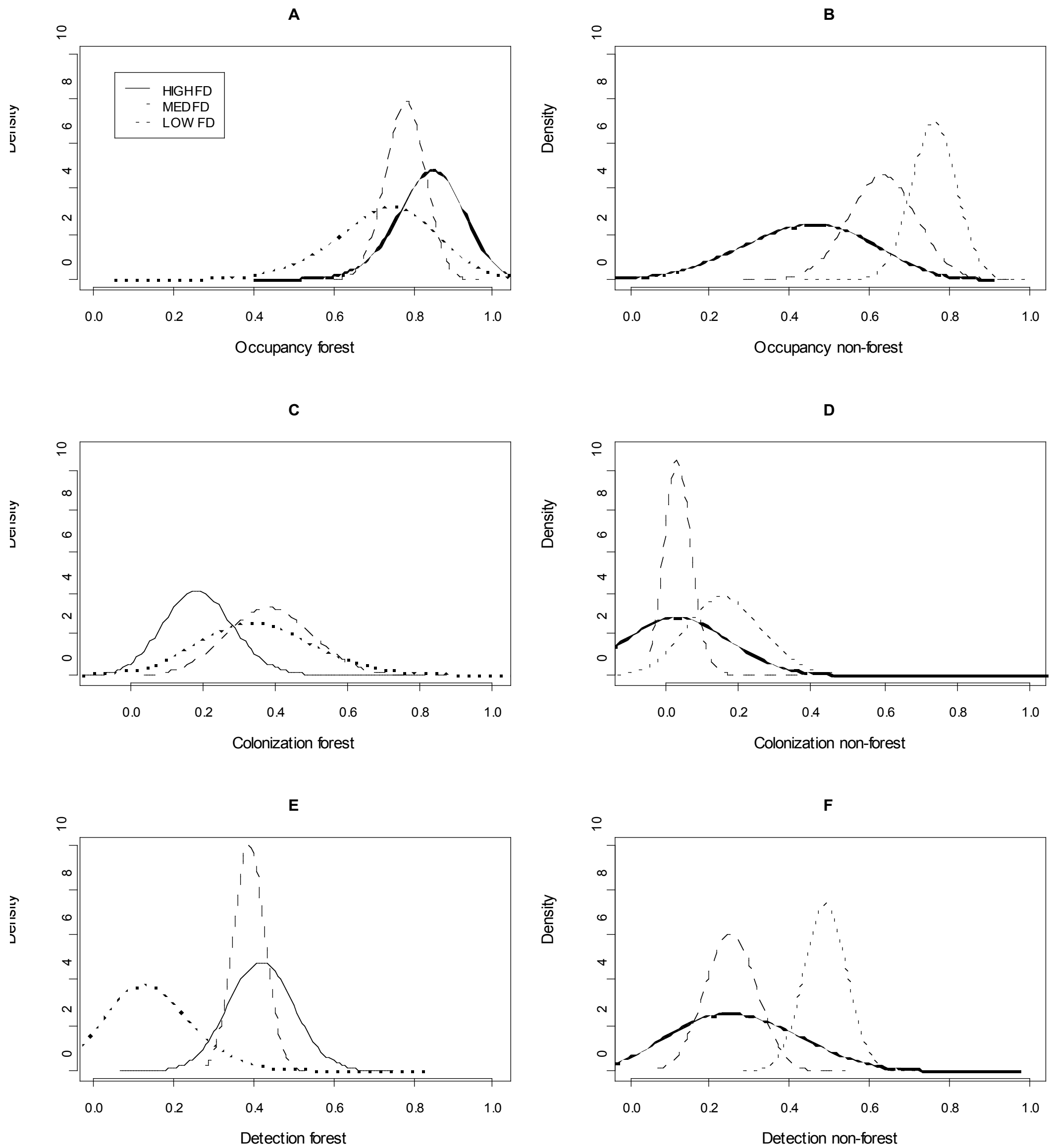

Figure 5. Kernel density plots of the posterior distributions of estimated means for the hyperparameters of occupancy (A-B), colonization (C-D), and detection (E-F) of forest and non-forest respectively, as estimated using the hierarchical community model. Each plot represents the distribution of the estimated mean across each category of degree of forest dependency: HIGH, MED and LOW FD (see *Methods: Classification of forest dependency*).

This is further demonstrated by no apparent differences in mean species-specific estimates of occupancy in forest habitats based on prior categorization of degree of forest dependency (Fig. 6a-c). The posterior distributions of mean occupancy in non-forest were also high, but did not show the same degree of overlap as in forest among forest dependency categories (Fig. 6a-c). As predicted, the highest mean occupancy in non-forest was observed for LOW FD species, followed by MED FD species, and HIGH FD species showing the lowest mean response (Fig. 5b with $\mu_{\mu 2\_high} < \mu_{\mu 2\_med} < \mu_{\mu 2\_low}$). This pattern was also evident from the differences in species-specific occupancy estimates for non-forest based on category of forest dependency (Fig. 2a-c). In other words, the probability of continued occupancy in forest was high across all species, but only continued occupancy of non-forest varied as predicted by a species' prior categorization of forest dependency.

Colonization of forest vs. non-forest

Forest habitats had overall high mean colonization across species for all groups of forest dependency, but estimates for the MED FD category broadly overlapped with the LOW FD category, and distributions tended to be higher in comparison to the HIGH FD group (Fig. 5c with $\theta_{\theta 1\_high} > (\theta_{\theta 1\_med} \sim \theta_{\theta 1\_low})$). The distributions of mean colonization in non-forest were low overall, with the highest estimates for the LOW FD category, and much lower and overlapping estimates for MED FD and HIGH FD (Fig. 5d with $(\theta_{\theta 2\_high} \sim \theta_{\theta 2\_med}) < \theta_{\theta 2\_low}$). This pattern was supported by species-specific estimates having low overall means of colonization in non-forest habitats (Fig. 6a-c).

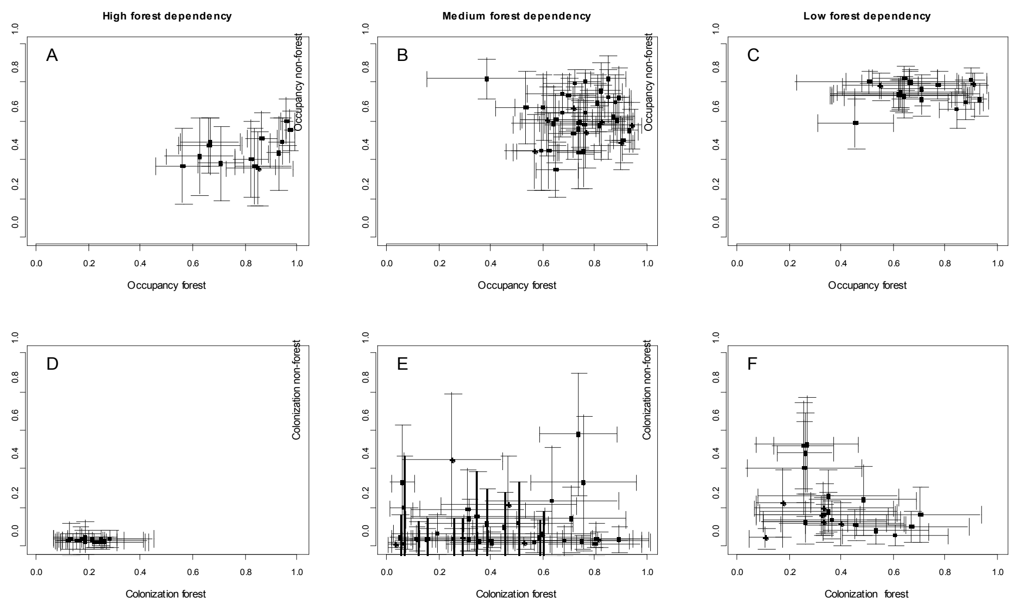

Figure 6. Species-specific mean posterior estimates of occupancy (A-C) and colonization (D-F), of forest and non-forest, as estimated using the hierarchical community model. The estimates are plotted by prior categorization of degree of forest dependency: high, medium and low (see *Methods: Classification of forest dependency*). The bars represent the standard deviations (SD) of each posterior mean estimate.

Occupancy and Colonization

Contrary to our expectations, species-specific mean colonization probabilities for forest and non-forest habitat types were not a function of their respective occupancy probabilities for either habitat (Fig. 7). In other words, the probability of being continually present in forest or non-forest has poor predictive power on the probability of opportunistic use of the same. We found high variability in species-specific colonization probabilities of forest habitats within the small range of occupancy probabilities in forest and non-forest (Fig. 7a,b). We found a similar pattern in colonization probabilities of non-forest in relation to forest occupancy (Fig. 7c), although showing a lesser amount of variability in responses. Mean species-specific colonization probabilities of non-forest appeared to increase in variability as the probability of non-forest occupancy increased (Fig. 7d).

Detection

Mean species-specific estimates of detection were less than 1.0 for all species in both forest and non-forest habitats (Appendix D). Distributions of mean detection probabilities in forest habitats for the HIGH and MED FD categories broadly overlapped, and were higher than for the LOW FD species group (Fig. 5e with $v_{v1\_high} \sim v_{v1\_med} > v_{v1\_low}$). In non-forest habitats, distributions of mean detection probabilities for HIGH and MED FD species group again overlapped, but were lower than estimates for the LOW FD species groups (Fig. 5f with $v_{v2\_high} \sim v_{v2\_med} > v_{v2\_low}$). This suggests that our analyses of occupancy and colonization across habitat types at the species and group level would have been greatly biased if detection had been left uncorrected.

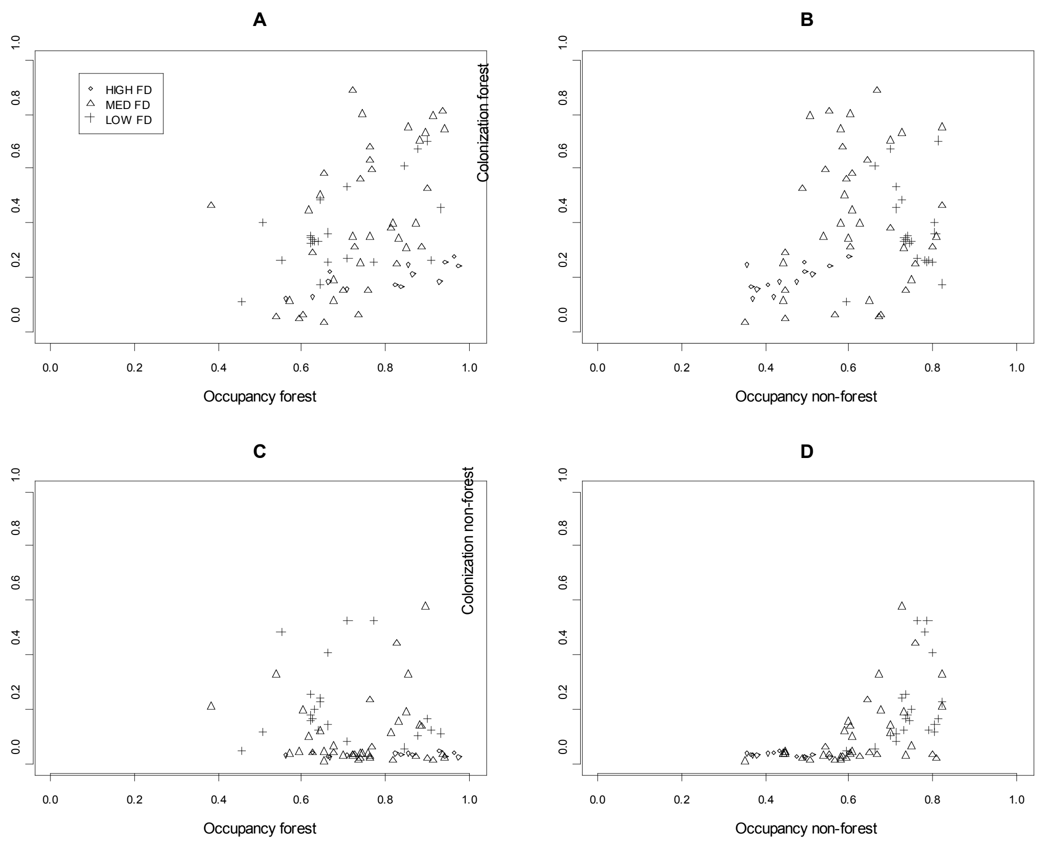

Figure 7. Species-specific mean posterior estimates of colonization as a function of occupancy for forest and non-forest as estimated using the hierarchical community model. The symbols represent prior categorization of degree of forest dependency: HIGH FD, MED FD and LOW FD (see *Methods: Classification of forest dependency*).

Discussion

We applied a dynamic, multi-species hierarchical community model to estimate probabilities of mean occupancy and colonization of both focal and intervening matrix habitat types, accounting for potential differences in detectability. Our results showed that the prior categorization of degree of forest dependency of species was a poor indicator overall of occupancy and colonization, and instead found higher than expected use of forest across species. Most importantly, our model yielded species-specific estimates we used to identify the species, specific to this region, that are likely to be most vulnerable to habitat loss and fragmentation.

Occupancy and colonization: forest is favored

We found mean occupancy and colonization of forest habitats to be high across all categories of forest dependency, relative to non-forest (Fig. 5a-d). Our results with regards to the distribution of mean occupancy in forest, and colonization of forest and non-forest, did not follow predicted patterns based on prior categorization of species as HIGH, MED and LOW FD, but distributions of mean occupancy in non-forest did (Fig. 1a-d). Our species-specific estimates of mean occupancy of forest or non-forest habitat types also had poor predictive power to characterize the colonization of forest habitat types (Fig. 7a,b). In other words, regardless of the habitat type with which a species is mainly associated with, there is a higher than expected level of opportunistic use of forest across species. Most importantly, the range of species-specific estimates of occupancy and colonization of forest for HIGH FD included estimates of species in MED and LOW FD categories, suggesting that current continued and opportunistic use of forest for species in the latter categories would be underestimated if based just on prior categorization of forest dependency (Fig. 7a,b).

Species classified with lower forest dependencies – considered to be resilient to reductions of forest habitat based on prior association to open habitat types – appear to associate with forest more than expected, both opportunistically and longer-term. This highlights the importance of remnant forest habitats for long-term persistence of the bird community in a fragmented landscape, like small forest patches and riparian strips, even for species typically associated with open and degraded land uses.

Habitat-specific detectability

All species that we were able to analyze had mean estimates of detection probabilities that were < 1.0 (Appendix D). Detectability also differed widely between habitats by category of forest dependency (Fig 5e,f), showing great variability in species-specific estimates of detectability within, and between, habitat types (Appendix C). Our comparison of occupancy dynamics would have been greatly biased had we not corrected for differences in detectability between species and habitat types. We suggest that future work account for differences in detectability among species and habitat types, specially in species-rich regions. This is even more strongly recommended for work contrasting occupancy, species richness or abundance between different habitat types, since any significant contrasts could be just artifacts of differences in detectability.

Implications for CE and BIDE approaches

We found that probability of occupancy of forest and non-forest habitats are not strong indicators of colonization probability of either habitat type (Fig. 7). In other words, the opportunistic use of different habitat types can not simply be determined by looking at which habitats a species is most associated. The large amount of variability in colonization rates also indicate that a true effective focal patch size would be difficult to estimate for all but a few species (Fig. 7a,c). For these species, colonization could potentially be a function of both nearby occupied focal and matrix habitats. The "island system" assumed under the CE approach will most likely be perceived only by species with high continued occupancy of forest habitats, and low probabilities of occupancy and colonization for non-forest.

Our results also suggest that colonization of matrix habitats in a heterogeneous landscape is not directly related to how likely a species is to remain in a habitat type (Fig. 7b), a factor usually attributed to focal patch area under the BIDE approach. If the latter is true, commonly used landscape metrics like patch area or isolation might not be good indicators of the likelihood of matrix colonization. Some species are also able to occupy both forest and matrix habitats, hence colonization of the matrix will not necessarily be detrimental. Similarly to the CE approach, species for which BIDE would accurately predict occupancy dynamics in a patchy environment would be species with high continued occupancy probabilities of focal habitat, and low occupancy and colonization probabilities of matrix habitats.

Validity of forest dependency categories

Ecological classifications, based on prior or published work, personal observations, or expert opinions, are widely used to subset species of interest from a community to test hypotheses on how animal populations are affected by habitat loss and fragmentation (Boulinier et al., 2001; Ferraz et al., 2007; Petit and Petit, 2003). Radford and Bennett (2007) and Schlossberg and King (2008) found that these classifications did not coincide with their results, and highlighted the need to test these widely accepted, potentially unreliable ecological classifications.

The probability of occupancy of forest and non-forest displayed predicted trends across species based on prior ecological categorization of forest dependency only for HIGH FD species, but had poor predictive power for species in the MED and LOW FD categories (Fig. 5a,b and Fig. 6a-c). We did not find predictable trends of colonization of forest and non-forest habitats again for species in the MED and LOW FD categories (Fig. 5c,d). We conclude prior categorization of forest dependency has poor predictive power with regards to species responses to changes in amount and configuration of available habitat, as well as identifying which species or populations are of conservation concern.

Implications for conservation: identification of vulnerable species

A classification system based on presence or absence in matrix habitats has been previously suggested to predict which species will be most vulnerable to combined effects of habitat loss and fragmentation, and has improved the predictive power of patch occupancy models across species when included (Donald and Evans, 2006; Umetsu et al., 2008). But occupancy dynamics have also been shown to be highly landscape-specific, and to vary by region (Castellon and Sieving, 2006; Rhodes et al., 2008; Watson et al., 2008). Matrix habitat use could also be spatially-explicit, change at different scales, and/or be dependent on the relative proportions of habitat of interest at each scale (Flather and Bevers, 2002)Tubelis and Lindenmeyer, 2004). We suggest estimating occupancy dynamics, at appropriate spatial scales of focal and matrix habitats as a potential classification system of the subset of species most likely to be negatively affected by habitat loss and fragmentation. Consistent with CE and BIDE approaches, the most vulnerable species would be those with relatively high mean estimates of occupancy of forest, and low mean estimates of occupancy and colonization of non-forest. (Fig. 7b,c). Under these criteria, species of highest conservation concern make up 53% of the species in our analysis (n=39), including all of the species classified as highly forest dependent, as well as 22% of our species with a medium degree of forest dependency (n=16) (Appendix E).

Strengths and applicability of modeling approach

We were not able to get estimates for 139 of our detected species for which we had <30 observations across 5 sampling years. The proportions of the unmodeled species in each forest dependency category are similar to the proportions of the species we were able to analyze. For the 139 unmodeled species, 28% were in the high forest dependency category (n=39), 50% in the medium (n=69), and 24% in the low category (n=34), as compared to 17% (n=13), 53% (n=39), and 29% (n=21), respectively. Therefore, we suspect that our characterization based on this subsample of the occupancy dynamics of the avian community in this region is potentially representative of the community as a whole, although we believe that overall estimates for the unmodeled species are likely to be much lower. A large proportion of the 73 species we were able to make inferences on using our community level approach would otherwise have not been possible under more widely-used species-specific approaches (Zipkin et al., In review).

Conclusions

Regardless of species habitat type associations, we found a higher than expected level of continued occupancy and opportunistic use of forest across species in this community of tropical birds. Adequate protection of both extensive and remnant forest habitats will be crucial for the long-term persistence of the avifauna in this region, including those species that are not currently considered to be negatively influenced by land-use changes. All of the species in our community had less than perfect detection probabilities, and our comparison of occupancy dynamics between forest and non-forest would have been greatly biased had we not corrected for detection. We also consider that species' ecological classification of forest dependency was a poor indicator of overall occupancy dynamics for both habitats across species in the community. Consistent with CE and BIDE approaches, the species with high estimates of forest occupancy, and low estimates of non-forest occupancy and colonization, are likely to be the most vulnerable to the effects of habitat loss and fragmentation for this region. For our subset of the community, we found that 53% of the species in our analysis (n=39) fall under this category, compared to 31% (n= 23) if we were only to focus on species classified as highly forest dependent. We believe that our approach using a hierarchical model to estimate community and species-specific occupancy dynamics of focal and inter-patch matrix habitats is a powerful method to identify which species in a community, specific to a region of interest, are likely to be most vulnerable to the effects of habitat loss and fragmentation, at an appropriate scale of inference.

REFERENCES

Boulinier, T., J.D. Nichols, J.E. Hines, J.R. Sauer, C.H. Flather, and K.H. Pollock. 2001. Forest fragmentation and bird community dynamics: Inference at regional scales. *Ecology*. 82:1159-1169.

Castellon, T.D., and K.E. Sieving. 2006. Landscape history, fragmentation, and patch occupancy: Models for a forest bird with limited dispersal. *Ecological Applications*. 16:2223-2234.

Donald, P.F., and A.D. Evans. 2006. Habitat connectivity and matrix restoration: the wider implications of agri-environment schemes. *Journal of Applied Ecology*. 43:209-218.

Ferraz, G., J.D. Nichols, J.E. Hines, P.C. Stouffer, R.O. Bierregaard, and T.E. Lovejoy. 2007. A large-scale deforestation experiment: Effects of patch area and isolation on Amazon birds. *Science*. 315:238-241.

Flather, C.H., and M. Bevers. 2002. Patchy reaction-diffusion and population abundance: The relative importance of habitat amount and arrangement. *American Naturalist*. 159:40-56.

Petit, L., and D. Petit. 2003. Evaluating the importance of human-modified lands for neotropical bird conservation. *CONSERVATION BIOLOGY*. 17:687-694.

Rhodes, J.R., J.G. Callaghan, C.A. McAlpine, C. De Jong, M.E. Bowen, D.L. Mitchell, D. Lunney, and H.P. Possingham. 2008. Regional variation in habitat-occupancy thresholds: a warning for conservation planning. *Journal of Applied Ecology*. 45:549-557.

Schlossberg, S., and D.I. King. 2008. Are shrubland birds edge specialists? *Ecological Applications*. 18:1325-1330.

Umetsu, F., J.P. Metzger, and R. Pardini. 2008. Importance of estimating matrix quality for modeling species distribution in complex tropical landscapes: a test with Atlantic forest small mammals. *Ecography*. 31:359-370.

Watson, C.A., F.W. Weckerly, J.S. Hatfield, C.C. Farquhar, and P.S. Williamson. 2008. Presence-nonpresence surveys of golden-cheeked warblers: detection, occupancy and survey effort. *Animal Conservation*. 11:484-492.

CHAPTER 5

SHORTER AND COMPACT CANOPY LAYERS IN FOREST FRAGMENTS: FRAGMENTATION EFFECTS ON TROPICAL TREE SPECIES' COMPOSITION AND STRUCTURAL COMPLEXITY

Abstract

The detrimental effects associated with habitat loss and fragmentation pose the need to signal what measurable habitat variables are good indicators of reduced habitat quality of remnant habitats. Habitat quality can only be considered in relation to variables previously shown to significantly influence communities and populations of a group of interest. We focused on estimating changes in habitat quality of remnant forest fragments for a community of tropical birds in southwestern Costa Rica. We found a significant effect of reduced area on tree species composition and abundance of forest interior relative to pioneer species ($p < 0.0001$ for each). Therefore, forest fragmentation probably reduces habitat quality for this bird community through a reduction and change of tree-mediated food sources. We also found a significant effect on height in forest fragments relative to control sites ($t=5.88$, $p = 0.0001$), and there was strong support for this effect to vary dependent on the canopy strata of the tree ($t= 5.20$, $p < 0.0001$). We applied this model to generate predicted values of height for each strata type for forest fragments and control sites. Our results show that forest fragmentation has additional significant impacts on the structural complexity of remnant fragments through reductions in height of canopy strata. These effects were not significantly affected by distance from the edge. The increased degree of overlap between canopy strata is likely to reduce or eliminate microhabitats associated with these strata, and reduce resources linked to foraging and breeding sites. Therefore,

fragmentation of tropical forests could potentially reduce the quality of the habitat for tropical bird communities through changes in food resources and availability of microhabitats, as observed by changes in the structure and composition of the tree community. The ecological integrity of these fragments is likely to continue to deteriorate, and their long-term potential to serve as habitat for birds and other organisms is likely to decrease unless action is taken to mitigate these effects.

Introduction

There is little debate with regards to the detrimental effects of habitat loss and fragmentation on animal populations, although which specific habitat-related factors can be directly linked to population declines and extinctions remain largely unknown (Debinski and Holt, 2000; Ewers and Didham, 2006; Laurance et al., 2002). Research on fragmentation effects has mainly generated a set of habitat and landscape-level metrics that are linked with measures of habitat quality, like fragment shape and total amount of forest cover (Andren, 1994). Factors like patch size and isolation have been shown to be strong predictors of changes in composition and structural complexity of remnant vegetation community, and are extensively reviewed elsewhere (Fischer *et al.*, 2007; Laurance *et al.*, 2002; Prugh *et al.*, 2008). How changes in habitat variables of the remnant vegetation predicted by these metrics translate into reductions in habitat "quality" has received much less attention, leaving ecologists to often make assumptions with regards to which variables are stronger determinants of observed changes in populations or communities (Feeley and Terborgh, 2006; Franklin et al., 2002).

The relationship between area and species richness and composition is one of the most widely tested factors in fragmentation research, and signaled as the strongest predictor of richness and abundance of trees in both temperate and tropical regions

(Arroyo-Rodriguez and Mandujano, 2006b; Hill and Curran, 2003; Laurance et al., 2000b). But this effect of area is still open to debate, especially for tropical systems, given the complexity and diversity of the landscapes in which forest remnants are typically embedded (Cayuela *et al.*, 2006). Tropical regions are diverse and highly dynamic, and fragmentation effects on the "quality" of tropical forests might be best predicted by different patch and landscape-level metrics than those for more widely studied temperate forests. For example, fragmentation effects related to remnant forest edges (*edge effects*) in temperate regions are harder to detect in more heterogeneous landscapes, and they are proposed not to be as ecologically important (Harper *et al.*, 2005; Laurance, 2000; Laurance *et al.*, 2007). The relationship between patch isolation and tree communities has also proven difficult to determine in tropical forests, given the short time frame of most research, especially relative to time since disturbance (Hill and Curran, 2003). One of the few long-term and experimental fragmentation projects in the tropics found that effects of area and isolation varied strongly dependent on the composition of the surrounding matrix habitats (Laurance *et al.*, 2006; Nascimento *et al.*, 2006).

Changes in tree species richness and composition are only one aspect of fragmentation effects on forest quality. Fragmentation effects on the structural complexity of forests are commonly used as indicators of reduced habitat quality in temperate forests. Tropical forests, on the other hand, show greater variability in responses of fragmentation effects on structural complexity. For example, trees have been shown to increase in diameter at breast height (DBH) with increasing distance from the edge in forest fragments (Laurance *et al.*, 1998), although sometimes only bigger, thicker trees (DBH > 60 cm) show an increase in abundance with area (Arroyo-Rodriguez and Mandujano, 2006a). Basal area has been shown to increase with canopy cover (Pearman, 2002), is overall greater in larger forests

(Muthuramkumar *et al.*, 2006), but sometimes differences are only detected in larger trees (DBH > 60 cm) (Arroyo-Rodriguez and Mandujano, 2006a). Tree density also increases in larger tropical forests remnants (Muthuramkumar *et al.*, 2006), as well as canopy height (Matlock and Edwards, 2006). This high degree of variability in responses to fragmentation effects on structural complexity is widely attributed to the fact that tropical forests are chronically disturbed, and changes related to disturbance might be more difficult to detect (Laurance, 2008).

Fragmentation effects on tree species composition and structural complexity of tropical forests will only be indicative of reductions in “quality” when carried out in the context of changes in habitat variables shown to directly influence composition and abundance of a population or community of interest (Arroyo-Rodriguez et al., 2008). At a species-level, reductions in habitat quality have been accurately derived by estimating fragmentation effects on the abundance and distribution of flora known to be key resources for a specific animal population (Arroyo-Rodriguez and Mandujano, 2006a; Zanette, 2001). At a community level, habitat-related measures known to influence the abundance or distribution of a given group or taxa of concern can be applied. For tropical avian communities, structural complexity of forests (*i.e.* basal area, canopy height, tree species density) have been widely linked to species diversity (Bibby, 1992; Hughes et al., 2002; Matlock and Edwards, 2006). By and large, previous work has pointed to canopy height as the best overall predictor of bird species richness, with canopy cover and basal area having a more variable effect (Bibby, 1992; Matlock and Edwards, 2006).

To further our understanding of habitat fragmentation effects on tropical forest and their animal communities, we focused on estimating changes in habitat quality for tropical birds in southwestern Costa Rica. The avian community in this region has been widely studied, and fragmentation effects have been shown on both community composition and population dynamics of a wide range of bird species (Borgella and Gavin, 2005; Hughes et al., 2002; Matlock and Edwards, 2006). The floristic composition of this region is also well known, although fragmentation effects on forest composition and structure have yet to be estimated. We estimated differences in tree species composition, abundance, and structural complexity between forest fragments and continuous tracts of a mid-elevational tropical forest. We tested for an effect of area on total number of tree species, and relative abundance of species classified as forest interior or pioneer. We also tested for differences in heights among canopy strata to estimate fragmentation effects on structural complexity. The relationship between increasing canopy height and bird abundance and composition has been shown consistently across tropical regions, but the actual effects on height in relation to canopy structure (*i.e.* strata) are not as well defined (Matlock and Edwards, 2006; Meynard and Quinn, 2008). The stratification of canopy trees in tropical forests is one of the main drivers of structural complexity, but fragmentation effects on relative heights of strata remain largely unknown. We also modeled height of strata relative to distance from the edge of the forest fragments. A reduction in tree species richness and abundance, coupled with changes in species composition, will be indicative of a lowered habitat quality through a reduction in food sources and habitat heterogeneity. Most importantly, fragmentation has significant impacts on the structural complexity of remnant fragments through reductions in height of canopy strata. The increased degree of overlap between canopy strata is likely to reduce or eliminate microhabitats associated with these, and reduce resources linked to foraging and breeding sites. Both of these effects are highly likely to affect tropical bird populations in this region.

Materials and Methods

Study Site

The Coto Brus Valley is located in the southwest of Costa Rica, on a depression between the Cordillera Talamanca and Fila Costera. Further southwest, the Valley meets a large limestone formation which is part of the Fila Costera and which descends abruptly and almost vertically from 1500 to 0 masl towards the coastal lowlands of Golfito and the Osa Peninsula. There is a well defined wet or rainy season (April to December) as well as a dry season (January to March), with at least 3-4 dry months every year. Mean annual rainfall is 3804 mm, although it can range from 2860-5617 mm per year. Mean temperature varies slightly and ranges from 20 to 22˚C.

The forests in this system are classified as premontane and transitional premontane wet forest based on Holdridge's Life Zone System (1947). The region was largely deforested for agriculture in the 1950's, leaving behind a heterogeneous agricultural landscape dominated by coffee plantations, banana plantations, ornamental garden plots, pine tree (*Pinus caribaea*) and terminalia (*Terminalia amazonia*) plantations, cattle pastures, abandoned pastures, and small forest fragments. We sampled six remnant forest fragments in this region: Brasilia (11 ha; 980 masl), Cedeño (12,5 ha; 1095 masl), Sabalito (18 ha; 910 masl), Fragment 9 (20 ha; 1190 masl), Fragment 5 (25 ha; 1490 masl), and Loma Linda (27 ha; 1085 masl). The selected control sites were the Las Cruces Biological Station Forest Reserve (262 ha; 1222 masl), La Amistad National Park- Altamira Station (400 000 ha; 1567 masl), and the Guaymi Indigenous Reserve (4, 200 ha; 1393 masl) (Figure 8; Table 7).

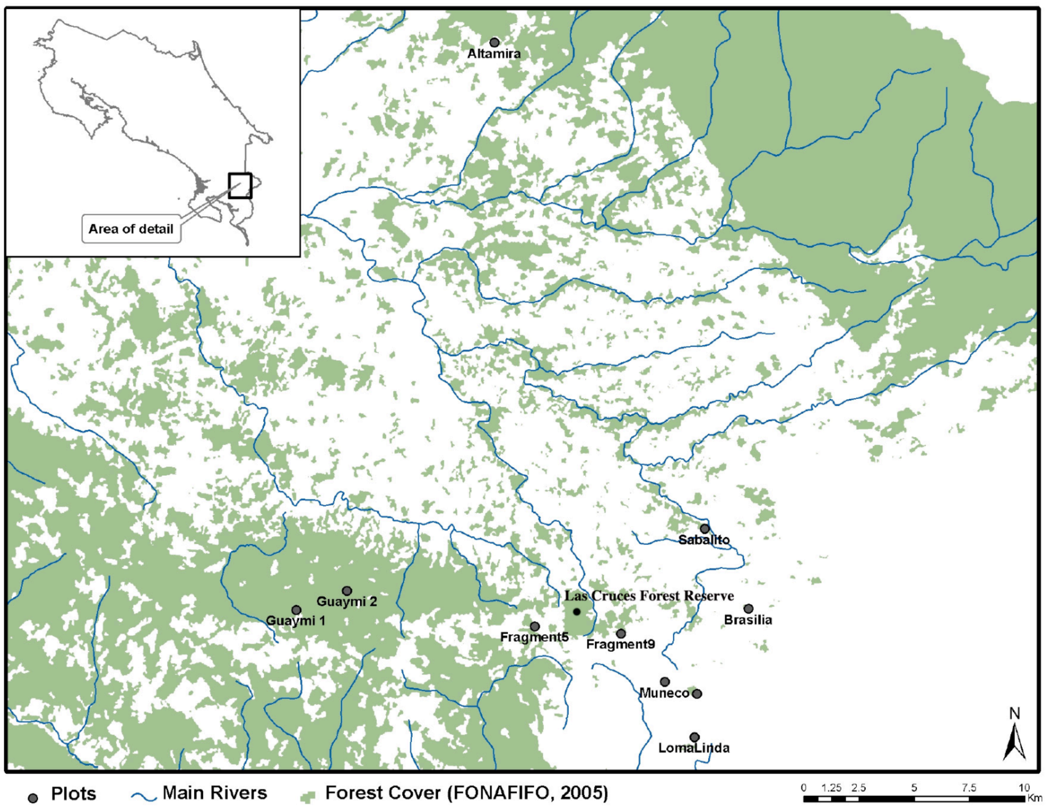

Figure 8. Map of the study region, with circles representing sites where sampling plots were set up. Green represents forest cover and white represents non-forest. Map courtesy of the Las Cruces Biological Station (Victor Milla).

Table 7. List of forest fragments and larger continuous forests used in this study by type of site, forest or control site (F or C), area, name of site, and altitude.

Type	Area (ha)	Site	Altitude (masl)
F	11	Brasilia	980
F	15	Cedeno	1095
F	20	Sabalito	910
F	20	Fragment 9	1190
F	25	Fragment 5	1490
F	35	Loma Linda	1085
C	262	Las Cruces Forest Reserve	1222
C	5600	Guaymi Indigenous Reserve	1393
C	400,000	La Amistad National Park	1567

Sampling design and data collection

The size of the forest fragments was estimated using digitized aerial photographs in program Manifold 7x (Manifold.net). In each fragment, three evenly-distanced sampling rings were digitally created with the same software from the forest edge to the interior, and classified in a distance class. The first ring (Class 1= edge ring) was located 20 meters from the forest edge, the second ring (Class 2 = interior ring) 70 meters from the edge, and the third ring (Class 3 = core ring) 120 meters from the edge. Within each sampling ring, three different size plots were established: 100m2, 400m2, and 900m2. Sampling area varied according to fragment size but ranged from 3-4% of the total fragment area. The distance between plots is variable; it varies with the topographic conditions but was never less than 50 meters. In the field, the plots were located with a Garmin 60Csx GPS Unit, with a positional error of 4-11 meters. Within the plots, we recorded for every tree greater than DBH ≥10 cm the following: species, DBH, height (estimated), and position in the vertical strata. We classified strata as: (1) suppressed, (2) intermediate, (3) dominant, and (4) emergent (Dawkins 1958). Height was measured using a clinometer, with the measurement taken at least 30 m from the base of the tree.

In the control sites it is logistically inefficient to implement this sampling methodology, mainly due to limited access given the topology of the control sites. Therefore, control sites were sampled in systematically designed transects, distanced no less than 100 meters from each other. Within each transect, three different size plots were established: 100m2, 400m2, and 900m2. It is assumed then that control sites are not affected by edge effects, and all plots were situated well beyond the 300m where edge effects have been shown in tropical forests (Laurance *et al.*, 2002).

Species richness and fragment area

We used a multivariate analysis of variance (MANOVA) to test for species-area relationships. We estimated patterns of species composition across control sites and forest fragments using a non-metric multidimensional scaling (NDMS). Pearson's correlation coefficient (r) was used to investigate the relationship between species' relative abundances and NMDS axes. The effect of fragment area was fit into the ordination by means of generalized additive models.

Structural complexity

An analysis of covariance (ANCOVA) was conducted to assess the effect of forest fragmentation on the dependent variable of canopy height. We used the independent variables of canopy strata class and the distance from edge class as an interaction term, to test if mean height for each canopy strata class was dependent on the distance from the edge of the forest fragment. We also included the terms of elevation and DBH to control for effects of tree thickness on height. Tree height and DBH were not highly correlated. Elevation is also successfully used as a covariate for habitat variables that vary by altitude in highly topographic systems. The independent variables for all of the data were canopy strata class, elevation and DBH log, to estimate mean height for each canopy strata class. These values were used to test for differences in means of canopy strata height between forest and control sites. Normality and homoscedasticity were checked and resulted to be substantially improved by the log transformations for both forest fragments and control site analysis. All statistical tests were carried out using Program R (Team, 2005). The best formula-based model was selected for each ANCOVA using Akaike's Information Criterion in a stepwise algorithm using the "step" function available in the Stats package in program R.

Results

A total of 2,532 trees with DBH > 10cm were measured and indentified to species (81%), genus (10%), family (6%), or unidentified (3%). A summary of the most common species and their ecological attributes are presented in Appendix E.

Species richness

The total number of species significantly increased with fragment area ($p < 0.0001$ for each) (Figure 9). There were 24 species that showed a significant negative correlation with decreasing fragment area (NMDS axis 1), with 70% of these species previously classified as forest interior species (Figure 10). The rest of the species that showed positive correlations with decreasing fragment area are typically classified as pioneer species, more related to disturbed and regenerating forests (Vilchez-Alvarado, *pers. comm*).

Effects on height of canopy strata by distance from edge

Individual trees with at least one missing observation were eliminated for all subsequent analyses. Here, we present results from 2,291 sampled trees, out of which 820 were in control sites, and 1,471 were in forest fragments. The ANCOVA test for differences in height among strata relative to the distance from the forest fragments showed strong support for our model (R squared = 0.67, $p < 0.0001$). As expected, there were significant positive effects of canopy strata ($t=14.19$, $p < 0.0001$) and DBH ($t=21.76$, $p < 0.0001$) on height. There was a significant negative effect on height and elevation ($t=8.299$, $p < 0.0001$). There was a positive effect on height with increasing distance from the edge ($t=3.38$, $p = 0.0001$), but there was no support for this effect to depend on the canopy strata type ($t=1.66$, $p = 0.1$). We applied this model to generate predicted values and 95% confidence intervals for height for each stratum, for each

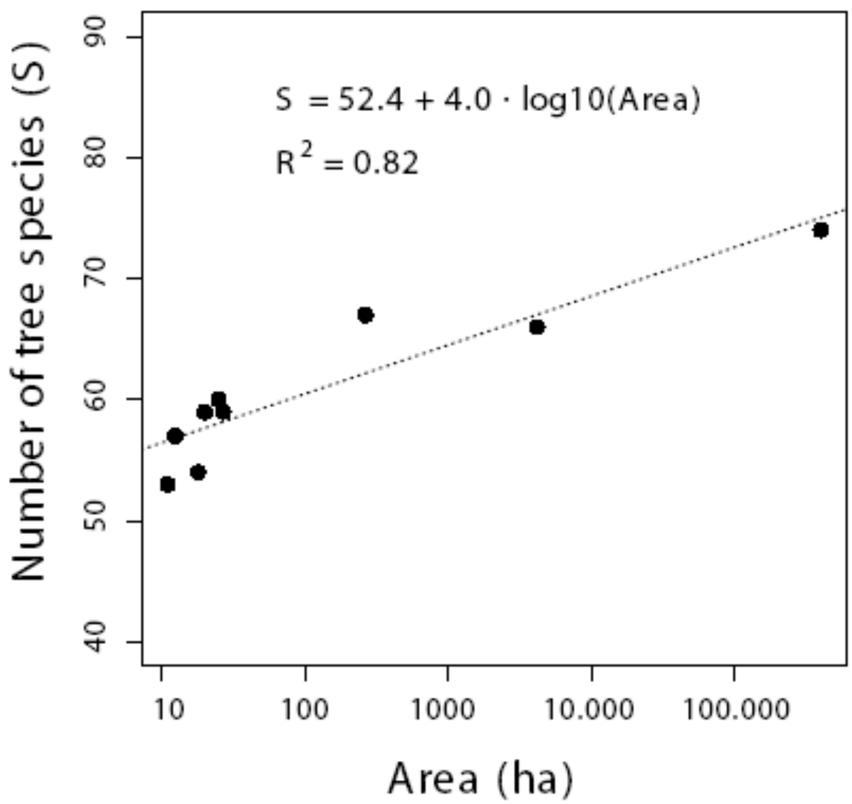

Figure 9. Total number of species as a function of area of forest fragment, based on six forest fragments and three larger control sites.

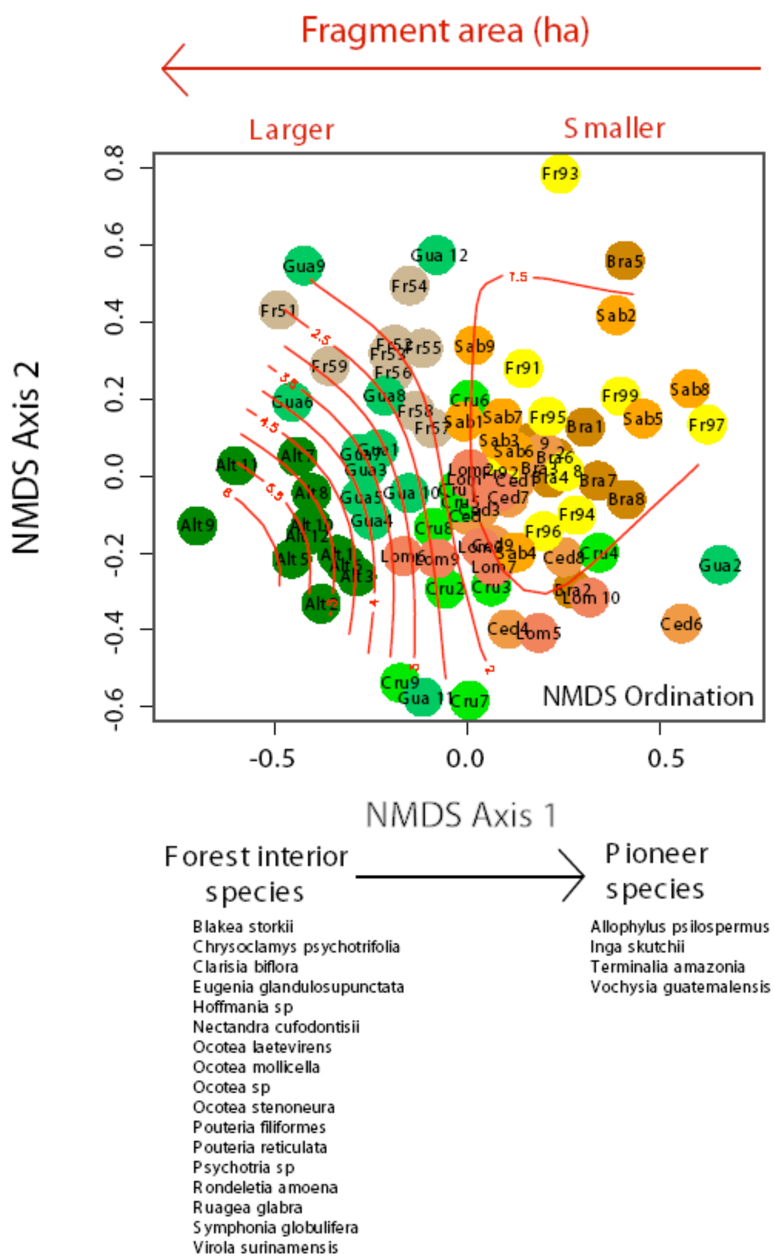

Figure 10. The effect of area of forest (NMDS Axis 1) on species abundance (NMDS Axis 2) in relation to species composition of forest interior and pioneer species.

Table 8. Predicted values for height for each strata, at average DBH and altitude, and 95% upper and lower confidence intervals, for each distance class from the edge of the forest fragments: Class 1:20 m , Class 2: 70 m, Class3: 120 m.

Dist. Class	Strata	Height	95% CI Lower	95% CI Upper	Mean Altitude	Mean DBH
1	1	8.56	8.19	8.95	1182.58	21.93
1	2	11.36	11.09	11.62	1182.58	21.93
1	3	15.07	14.73	15.41	1182.58	21.93
1	4	19.99	19.15	20.88	1182.58	21.93
2	1	9.17	8.84	9.51	1182.58	21.93
2	2	11.96	11.75	12.18	1182.58	21.93
2	3	15.61	15.36	15.87	1182.58	21.93
2	4	20.37	19.70	21.07	1182.58	21.93
3	1	9.82	9.33	10.34	1182.58	21.93
3	2	12.60	12.28	12.94	1182.58	21.93
3	3	16.18	15.74	16.63	1182.58	21.93
3	4	20.76	19.69	21.90	1182.58	21.93

class of distance from edge, under mean DBH and elevation (Table 8). Although our model showed a significant effect of distance on height, we consider that this difference might not be biologically meaningful (Figure 11). For example, predicted heights for the lower strata closest to the edge (height = 8.55 (8.18 – 8.95)) differed by less than a meter, or less than 10% of total height, from the predicted heights of the same strata in the forest interior (height = 9.8 (9.31 – 10.33)). Therefore, we combined all species sampled in both fragments and continuous forest control sites for subsequent analysis.

Effects on height of canopy between fragment and control sites

The ANCOVA test used to determine if height among strata varied between forest fragments and control sites showed strong support for our model (R squared = 0.67, $p < 0.0001$). Again, we had the expected significant positive effects of canopy strata ($t=26.96$, $p < 0.0001$) and DBH ($t=22.30$, $p < 0.0001$) on height. There was still a significant negative effect on height and elevation ($t=3.819$, $p = 0.0001$). We found a significant effect on height dependent on the type of site where the tree was sampled: forest fragment or control site ($t=5.88$, $p = 0.0001$), as well as strong support for this effect to depend on the canopy strata type ($t= 5.20$, $p < 0.0001$).

We applied this model to generate predicted values of height, with 95% confidence intervals, for each strata and each type of study site, forest fragment or control, under mean DBH and elevation (Table 9). We found that the observed differences in heights among strata were biologically relevant. Control sites depict a profile typically associated with tropical forests: clearly defined canopy layers, or strata, with tall emergent trees, and sub-canopy and understory (Figure 12a). In contrast, we found that forest fragments have less well defined canopy layers, with taller trees in the lower sub-canopy layers, the upper canopy showing similar height to

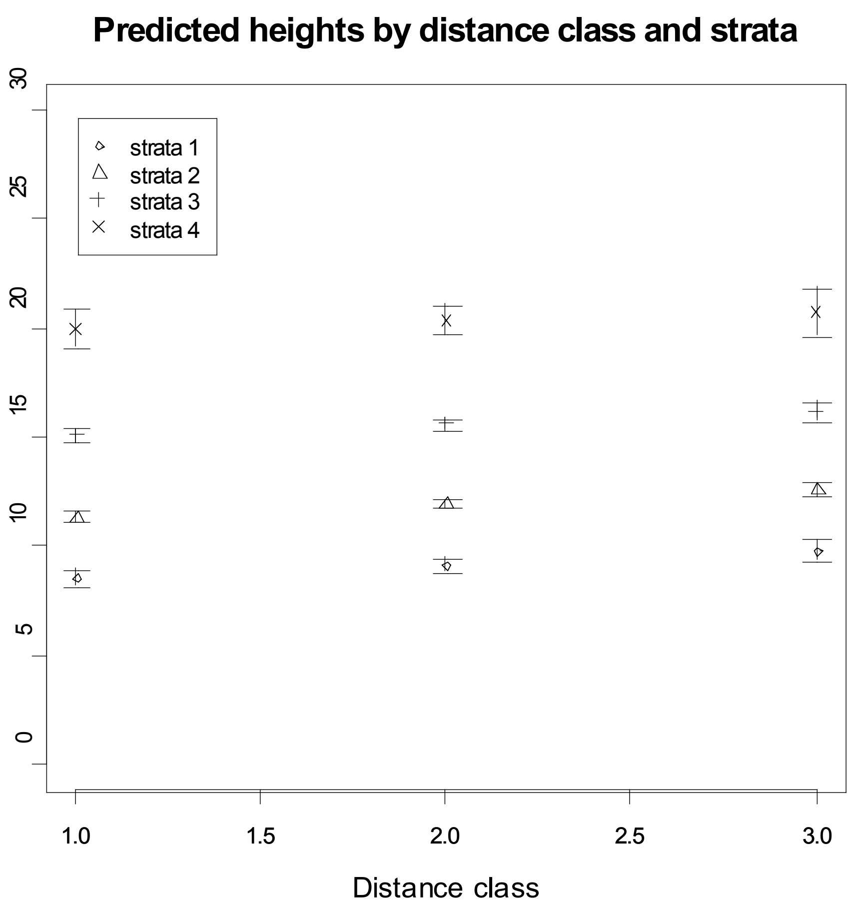

Figure 11. Predicted heights in meters of each canopy strata under the ANCOVA model for forest fragments, under mean altitude and DBH.

Table 9. Predicted values for height by strata, and 95% upper and lower confidence intervals, for both forest fragments and control sites.

Site type	Strata	Height	95% CI Lower	Upper	Mean Altitude	Mean DBH
F	1	8.72	8.41	9.04	1265.38	22.57
F	2	11.64	11.42	11.87	1265.38	22.57
F	3	15.54	15.27	15.81	1265.38	22.57
F	4	20.74	20.08	21.42	1265.38	22.57
C	1	7.60	7.31	7.90	1265.38	22.57
C	2	10.95	10.71	11.19	1265.38	22.57
C	3	15.78	15.32	16.25	1265.38	22.57
C	4	22.74	21.60	23.94	1265.38	22.57

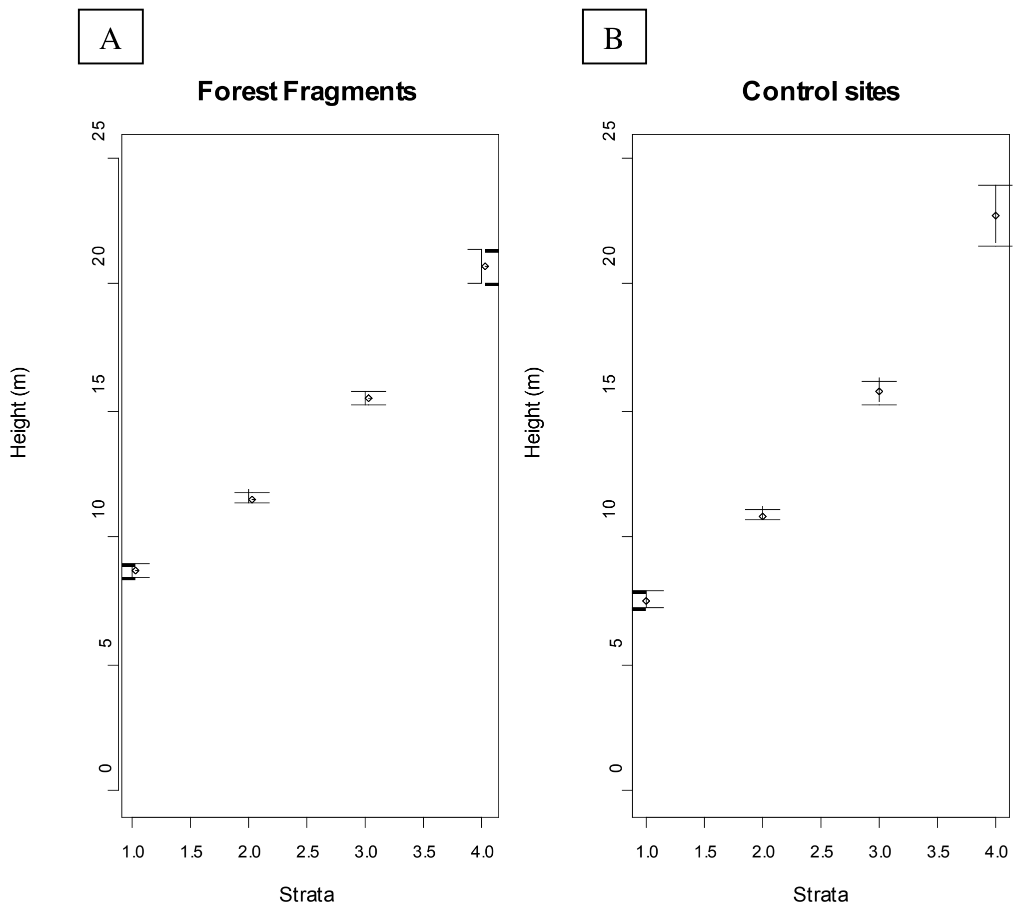

Figure 12. Predicted values for height for each strata, for forest fragments (A) and control sites (B), under mean DBH and altitude, showing 95% CI.

control sites, but with significantly shorter emergent trees (Figure 12b).

Discussion

The detrimental effects associated with habitat loss and fragmentation pose the need to signal what measurable habitat variables are good indicators of reduced habitat quality of remnant habitats. Fragmentation effects on species composition and structural complexity of the flora community in remnant fragments can only be indicative of a reduction in "habitat quality" when considered in relation to a specific taxonomic group known to be significantly affected by the observed changes. We found that species composition and abundance was significantly affected by forest fragmentation. This reduction and change in composition of food sources related to tree species is likely altering habitat quality for the associated forest bird community in the region. Most importantly, forest fragmentation is significantly altering the structural complexity of remnant forest fragments through reduced stratification of the canopy. This increased in the degree of overlap between canopy strata is likely to alter or eliminate associated microhabitats, and reduce resources linked to foraging and breeding sites for forest birds.

Fewer and different food sources

The reduction in species richness in forest fragments is expected, since tropical tree species have shown a tendency to be aggregated, and thus smaller areas will by default present lower species richness (Condit *et al.*, 2000). The phenology of most tropical tree species is largely unknown, but evidence suggests a high degree of temporal and seasonal variability in fruit production, with most production occurring in bursts of activity (Vanschaik et al., 1993). Approximately 70-94% of fruit biomass is produced by woody plant species in tropical forests (Jordan, 1992), and changes in the frequency and timing of fruit production in tree species by environmental factors has been shown to cause famine events in vertebrate tropical species (Wright et al, 1999). We found that forest fragments have fewer tree species that vary highly in the timing of food production. Fragmentation is likely lowering habitat quality through a reduction in supply of fruit, and related arthropod communities, resulting in changes in the amount and sources of food for the bird community.

Shorter trees and overlapping canopy strata

The reduction in overall canopy height and stratification is likely having profound effects on the bird community through a reduction in key microhabitats associated with the different levels of the canopy, likely used for nesting and foraging by the bird community. The repercussions of reduced stratification in canopy structure are likely impacting other groups of organisms in the forest. Structural complexity in forest habitats is one of the main determinants of species diversity. For example, tropical insect and mammal communities have stratified patterns of distribution concordant with canopy strata (Cunha and Vieira, 2002; Leite et al., 1996).

There are several potential drivers for the observed effects on height and related impacts on canopy structure. Increased mortality of emergent trees in forest fragments has been found in lowland Amazonian forests (Laurance *et al.*, 2000a). This increase in mortality is likely changing the dynamics of light gap dynamics, allowing for fast growing, pioneer species to become established. Canopy height changes in mature tropical forests were recently shown to be at a steady-state equilibrium (Kellner et al., 2009), and an increase in disturbance and tree mortality is likely to generate a left-skewed distribution of canopy height change, resulting in the observed overall reduction in canopy height. Given tree mortality is likely to be influenced by changes in nearby canopy structure (Batista and Maguire, 1998), the changes are likely to remain altering tree species composition and structure in the future.

Conclusions

Our results suggest that fragmentation of tropical forests strongly impacts habitat quality of remnant forest fragments for associated bird communities, through a reduction in food resources and availability of microhabitats driven by changes in the structure and composition of the tree community. The ecological integrity of these fragments is likely to continue to deteriorate, and their long-term potential to serve as habitat for birds and other organisms is likely to decrease, unless action is taken to mitigate these effects. For example, increasing the degree of connectivity between fragments and larger tracts of forest might facilitate seed dispersal, and enhance the re-generation of forest interior species. Future work should address the mechanisms driving structural changes and test for sources of emergent tree mortality

REFERENCES

Andren, H. 1994. Effects Of Habitat Fragmentation On Birds And Mammals In Landscapes With Different Proportions Of Suitable Habitat - A Review. *Oikos*. 71:355-366.

Arroyo-Rodriguez, V., and S. Mandujano. 2006a. Forest fragmentation modifies habitat quality for Alouatta palliata. *International Journal of Primatology*. 27:1079-1096.

Arroyo-Rodriguez, V., and S. Mandujano. 2006b. The importance of tropical rain forest fragments to the conservation of plant species diversity in Los Tuxtlas, Mexico. *Biodiversity and Conservation*. 15:4159-4179.

Arroyo-Rodriguez, V., S. Mandujano, and J. Benitez-Malvido. 2008. Landscape attributes affecting patch occupancy by howler monkeys (Alouatta palliata mexicana) at Los tuxtlas, Mexico. *American Journal of Primatology*. 70:69-77.

Batista, J.L.F., and D.A. Maguire. 1998. Modeling the spatial structure of topical forests. *Forest Ecology and Management*. 110:293-314.

Bibby, C.J. 1992. Conservation of Migrants on Their Breeding Grounds. *Ibis*. 134:29-34.

Borgella, R., and T.A. Gavin. 2005. Avian community dynamics in a fragmented tropical landscape. *Ecological Applications*. 15:1062-1073.

Cayuela, L., D.J. Golicher, J.M.R. Benayas, M. Gonzalez-Espinosa, and N. Ramirez-Marcial. 2006. Fragmentation, disturbance and tree diversity conservation in tropical montane forests. *Journal of Applied Ecology*. 43:1172-1181.

Condit, R., P.S. Ashton, P. Baker, S. Bunyavejchewin, S. Gunatilleke, N. Gunatilleke, S.P. Hubbell, R.B. Foster, A. Itoh, J.V. LaFrankie, H.S. Lee, E. Losos, N. Manokaran, R. Sukumar, and T. Yamakura. 2000. Spatial patterns in the distribution of tropical tree species. *Science*. 288:1414-1418.

Cunha, A.A., and M.V. Vieira. 2002. Support diameter, incline, and vertical movements of four didelphid marsupials in the Atlantic forest of Brazil. *Journal of Zoology*. 258:419-426.

Debinski, D.M., and R.D. Holt. 2000. A survey and overview of habitat fragmentation experiments. *Conservation Biology*. 14:342-355.

Ewers, R.M., and R.K. Didham. 2006. Confounding factors in the detection of species responses to habitat fragmentation. *Biological Reviews*. 81:117-142.

Feeley, K.J., and J.W. Terborgh. 2006. Habitat fragmentation and effects of herbivore (howler monkey) abundances on bird species richness. *Ecology*. 87:144-150.

Fischer, J., D.B. Lindenmayer, S.P. Blomberg, R. Montague-Drake, A. Felton, and J.A. Stein. 2007. Functional Richness and Relative Resilience of Bird Communities in Regions with Different Land Use Intensities. *Ecosystems*. 10:964-974.

Franklin, A.B., B.R. Noon, and L. George. 2002. What is habitat fragmentation? *Studies in Avian Biology*:20-29.

Harper, K.A., S.E. Macdonald, P.J. Burton, J.Q. Chen, K.D. Brosofske, S.C. Saunders, E.S. Euskirchen, D. Roberts, M.S. Jaiteh, and P.A. Esseen. 2005. Edge influence on forest structure and composition in fragmented landscapes. *Conservation Biology*. 19:768-782.

Hill, J.L., and P.J. Curran. 2003. Area, shape and isolation of tropical forest fragments: effects on tree species diversity and implications for conservation. *Journal of Biogeography*. 30:1391-1403.

Holdridge, L.R. 1947. Determination of World Plant Formations from Simple Climatic Data. *Science*. 105:367-368.

Hughes, J., G. Daily, and P. Ehrlich. 2002. Conservation of tropical forest birds in countryside habitats. *ECOLOGY LETTERS*. 5:121-129.

Jordan, N. 1992. Path-Analysis of Local Adaptation in 2 Ecotypes of the Annual Plant Diodia-Teres Walt (Rubiaceae). *American Naturalist*. 140:149-165.

Kellner, J.R., D.B. Clark, and S.P. Hubbell. 2009. Pervasive canopy dynamics produce short-term stability in a tropical rain forest landscape. *Ecology Letters*. 12:155-164.

Laurance, W., T. Lovejoy, H. Vasconcelos, E. Bruna, R. Didham, P. Stouffer, C. Gascon, R. Bierregaard, S. Laurance, and E. Sampaio. 2002. Ecosystem decay of Amazonian forest fragments: A 22-year investigation. *Conservation Biology*. 16:605-618.

Laurance, W.F. 2000. Do edge effects occur over large spatial scales? *Trends in Ecology & Evolution*. 15:134-135.

Laurance, W.F. 2008. Theory meets reality: How habitat fragmentation research has transcended island biogeographic theory. *Biological Conservation*. 141:1731-1744.

Laurance, W.F., P. Delamonica, S.G. Laurance, H.L. Vasconcelos, and T.E. Lovejoy. 2000a. Conservation - Rainforest fragmentation kills big trees. *Nature*. 404:836-836.

Laurance, W.F., L.V. Ferreira, J.M. Rankin-De Merona, and S.G. Laurance. 1998. Rain forest fragmentation and the dynamics of Amazonian tree communities. *Ecology*. 79:2032-2040.

Laurance, W.F., H.E.M. Nascimento, S.G. Laurance, A. Andrade, R.M. Ewers, K.E. Harms, R.C.C. Luizao, and J.E.L. Ribeiro. 2007. Habitat fragmentation, variable edge effects, and the landscape divergence hypothesis. *PLoS ONE*. 2:1017-1371.

Laurance, W.F., H.E.M. Nascimento, S.G. Laurance, A. Andrade, J.E.L.S. Ribeiro, J.P. Giraldo, T.E. Lovejoy, R. Condit, J. Chave, K.E. Harms, and S. D'Angelo. 2006. Rapid decay of tree-community composition in Amazonian forest fragments. *Proceedings of the National Academy of Sciences of the United States of America*. 103:19010-19014.

Laurance, W.F., H.L. Vasconcelos, and T.E. Lovejoy. 2000b. Forest loss and fragmentation in the Amazon: implications for wildlife conservation. *Oryx*. 34:39-45.

Leite, Y.L.R., L.P. Costa, and J.R. Stallings. 1996. Diet and vertical space use of three sympatric opossums in a Brazilian Atlantic forest reserve. *Journal of Tropical Ecology*. 12:435-440.

Matlock, R.B., and P.J. Edwards. 2006. The influence of habitat variables on Bird Communities in Forest Remnants in Costa Rica. *Biodiversity and Conservation*. 15:2987-3016.

Meynard, C.N., and J.F. Quinn. 2008. Bird metacommunities in temperate South American forest: Vegetation structure, area, and climate effects. *Ecology*. 89:981-990.

Muthuramkumar, S., N. Ayyappan, N. Parthasarathy, D. Mudappa, T.R.S. Raman, M.A. Selwyn, and L.A. Pragasan. 2006. Plant community structure in tropical rain forest fragments of the western Ghats, India. *Biotropica*. 38:143-160.

Nascimento, H.E.M., A.C.S. Andrade, J.L.C. Camargo, W.F. Laurnce, S.G. Laurance, and J.E.L. Ribeiro. 2006. Effects of the surrounding matrix on tree recruitment in Amazonian forest fragments. *Conservation Biology*. 20:853-860.

Pearman, P.B. 2002. The scale of community structure: Habitat variation and avian guilds in tropical forest understory. *Ecological Monographs*. 72:19-39.

Prugh, L.R., K.E. Hodges, A.R.E. Sinclair, and J.S. Brashares. 2008. Effect of habitat area and isolation on fragmented animal populations. *Proceedings of the National Academy of Sciences of the United States of America*. 105:20770-20775.

Team, R.D.C. 2005. R: A language and environment for statictical computing. R Foundation for Statistical Computing, Vienna, Austria.

Vanschaik, C.P., J.W. Terborgh, and S.J. Wright. 1993. The Phenology of Tropical Forests - Adaptive Significance and Consequences for Primary Consumers. *Annual Review of Ecology and Systematics*. 24:353-377.

Zanette, L. 2001. Indicators of habitat quality and the reproductive output of a forest songbird in small and large fragments. *Journal of Avian Biology*. 32:38-46.

APPENDIX A

Appendix A. Multi-species hierarchical community model based on survey-specific detection/non-detection records. We implemented the model using a Bayesian approach with non-informative priors using program WinBUGS. We ran three chains of the model for 10,000 iterations each after a burn-in of length 10,000 and thinned the model by 10. We assessed convergence of the model using r-hat, which compares the variations within chains to the variation among the chains.

```
model {

   omega ~ dunif(0,1)

   alpha.mean1 ~ dunif(0,1)
   mualpha1 <- log(alpha.mean1) - log(1-alpha.mean1)
   alpha.mean2 ~ dunif(0,1)
   mualpha2 <- log(alpha.mean2) - log(1-alpha.mean2)

   tau.u ~ dgamma(0.1,0.1)
   tau.v ~ dgamma(0.1,0.1)
   tau.alpha1 ~ dgamma(0.1,0.1)
   tau.alpha2 ~ dgamma(0.1,0.1)

   theta0~dunif(-5,5)

 for(f in 1:3){
```

```
  w.mean1[f] ~ dunif(0,1)
  muw1[f] <- log(w.mean1[f]) - log(1-w.mean1[f])
  w.mean2[f] ~ dunif(0,1)
  muw2[f] <- log(th.mean2[f]) - log(1-th.mean2[f])
  }

for(g in 1:3){
  tau.w1[g]~dgamma(0.1,0.1)
  tau.w2[g]~dgamma(0.1,0.1)
  }

for(f in 1:3){
  u.mean1[f] ~ dunif(0,1)
  muu1[f] <- log(u.mean1[f]) - log(1-u.mean1[f])
  u.mean2[f] ~ dunif(0,1)
  muu2[f] <- log(u.mean2[f]) - log(1-u.mean2[f])
  }

for(g in 1:3){
  tau.u1[g]~dgamma(0.1,0.1)
  tau.u2[g]~dgamma(0.1,0.1)
  }

for(f in 1:3){
  v.mean1[f] ~ dunif(0,1)
  muv1[f] <- log(v.mean1[f]) - log(1-v.mean1[f])
```

```
  v.mean2[f] ~ dunif(0,1)
  muv2[f] <- log(v.mean2[f]) - log(1-v.mean2[f])
  }

 for(g in 1:3){
  tau.v1[g]~dgamma(0.1,0.1)
  tau.v2[g]~dgamma(0.1,0.1)
  }

 for (i in 1:(n+nzeroes)) {
  w[i] ~ dbin(omega, 1)

  u1[i]~dnorm(muu1[FD[i]],tau.u1[FD[i]])
  u2[i]~dnorm(muu2[FD[i]],tau.u2[FD[i]])

  w1[i]~dnorm(muw1[FD[i]],tau.w1[FD[i]])
  w2[i] ~ dnorm(muw2[FD[i]],tau.w2[FD[i]])

  v1[i]~dnorm(muv1[FD[i]],tau.v1[FD[i]])
  v2[i]~dnorm(muv2[FD[i]],tau.v2[FD[i]])
  alpha1[i] ~ dnorm(mualpha1, tau.alpha1)
  alpha2[i] ~ dnorm(mualpha2, tau.alpha2)

  for (j in 1:J) {
   logitpsi[j,i]<-  u1[i]*hab[j]  +  u2[i]*(1-hab[j])  +  alpha1[i]*elev[j] +
alpha2[i]*elev2[j]
```

```
    logit(psi[j,i])  <-logitpsi[j,i]
   mu.psi[j,i,1] <- psi[j,i] * w[i]
   Z[j,i,1] ~ dbin(mu.psi[j,i,1], 1)


 for (k in 1:K[j]){
    logit(theta[j,k,i,1]) <- v1[i]*hab[j]   +   v2[i]*(1-hab[j])
  mu.theta[j,k,i,1] <- theta[j,k,i,1]*Z[j,i,1]
  X[j,k,i,1] ~ dbin(mu.theta[j,k,i,1], 1)
     }
  for(t in 2:5){
    logit(muz[j,i,t])<-  u1[i]*hab[j]*(Z[j,i,t-1])  +  u2[i]*(1-hab[j])*Z[j,i,t-1]  +
alpha1[i]*elev[j] + alpha2[i]*elev2[j] +  w1[i]*(1-Z[j,i,t-1])*hab[j] + w2[i]*(1-
hab[j])*(1-Z[j,i,t-1])
   mu.psi[j,i,t]<-muz[j,i,t]*w[i]
   Z[j,i,t] ~ dbin(muz[j,i,t],1)


  for (k in 1:K[j]){
   logit(theta[j,k,i,t]) <- v1[i]*hab[j]   +   v2[i]*(1-hab[j])
   mu.theta[j,k,i,t] <- theta[j,k,i,t]*Z[j,i,t]
   X[j,k,i,t] ~ dbin(mu.theta[j,k,i,t], 1)
      }
     }
  }
 }
}
```

APPENDIX B

Appendix B. Forest dependency (FD) category (see *Methods: Classification of forest dependency*), number of observations (Count) for each species, as well as the mean, standard deviation (SD), and 95% posterior intervals for species-specific probabilities of occupancy of forest and non-forest, as estimated using the hierarchical community model.

				Occupancy Forest				Occupancy Non-forest			
Scientific name	Common name	FD	Sample	*Mean*	*SD*	*95% posterior interval*		*Mean*	*SD*	*95% posterior interval*	
Crypturellus soui	Little tinamou	3	74	0.71	0.11	0.49	0.93	0.71	0.08	0.51	0.85
Patagioenas speciosa	Scaled pigeon	2	57	0.65	0.13	0.39	0.90	0.61	0.13	0.30	0.83
Patagioenas nigrirostris	Short-billed pigeon	2	37	0.75	0.09	0.53	0.90	0.44	0.19	0.09	0.80
Leptotila verreauxi	White-tipped dove	2	51	0.38	0.23	0.06	0.85	0.82	0.11	0.57	0.97
Geotrygon chiriquensis	Chiriqui quail-dove	1	32	0.85	0.13	0.50	0.99	0.36	0.19	0.03	0.70
Aratinga finschi	Crimson-fronted parakeet	3	53	0.64	0.19	0.27	0.96	0.73	0.11	0.45	0.89
Piaya cayana	Squirrel cuckoo	2	56	0.83	0.09	0.58	0.96	0.60	0.19	0.16	0.90
Phaethornis guy	Green hermit	2	128	0.88	0.05	0.76	0.97	0.70	0.14	0.39	0.93
Phaethornis striigularis	Stripe-throated hermit	2	52	0.74	0.12	0.48	0.94	0.60	0.14	0.30	0.85
Campylopterus hemileucurus	Violet sabrewing	2	31	0.59	0.10	0.38	0.77	0.45	0.20	0.08	0.86
Amazilia decora	Charming hummingbird	2	55	0.74	0.08	0.56	0.89	0.44	0.19	0.10	0.80
Amazilia tzacatl	Rufous-tailed hummingbird	3	83	0.55	0.15	0.27	0.84	0.78	0.07	0.63	0.91
Trogon violaceus	Violaceous trogon	2	33	0.74	0.15	0.40	0.96	0.59	0.12	0.33	0.81
Momotus momota	Blue-crowned motmot	2	86	0.72	0.12	0.48	0.93	0.67	0.11	0.41	0.85
Ramphastos swainsonii	Chestnut-mandibled toucan	1	48	0.82	0.07	0.67	0.94	0.40	0.20	0.03	0.74
Picumnus olivaceus	Olivaceous piculet	2	30	0.76	0.15	0.41	0.97	0.64	0.21	0.17	0.96
Melanerpes rubricapillus	Red-crowned woodpecker	2	92	0.82	0.08	0.64	0.94	0.76	0.15	0.45	0.97
Automolus ochrolaemus	Buff-throated foliage-gleaner	2	54	0.87	0.08	0.64	0.97	0.62	0.12	0.37	0.84
Automolus rubiginosus	Ruddy foliage-gleaner	1	30	0.62	0.13	0.34	0.85	0.42	0.20	0.03	0.78
Sittasomus griseicapillus	Olivaceous woodcreeper	2	33	0.76	0.15	0.43	0.97	0.58	0.13	0.30	0.82
Xiphorhynchus erythropygius	Spotted woodcreeper	1	46	0.84	0.08	0.66	0.95	0.37	0.20	0.02	0.73
Lepidocolaptes souleyetii	Streak-headed woodcreeper	2	102	0.88	0.06	0.73	0.97	0.60	0.12	0.36	0.83
Thamnophilus bridgesi	Black-hooded antshrike	2	31	0.62	0.17	0.26	0.90	0.45	0.20	0.09	0.84
Dysithamnus mentalis	Plain antvireo	1	68	0.86	0.06	0.72	0.96	0.51	0.14	0.22	0.76
Formicarius analis	Black-faced antthrush	1	53	0.71	0.09	0.52	0.86	0.38	0.19	0.03	0.73
Myiopagis viridicata	Greenish elaenia	2	47	0.67	0.10	0.48	0.85	0.64	0.12	0.38	0.85
Elaenia flavogaster	Yellow-bellied elaenia	3	39	0.63	0.25	0.09	0.97	0.75	0.08	0.58	0.89
Mionectes oleagineus	Ochre-bellied flycatcher	2	53	0.62	0.10	0.40	0.82	0.60	0.18	0.19	0.91
Zimmerius vilissimus	Paltry tyrannulet	2	168	0.85	0.07	0.70	0.96	0.82	0.12	0.54	0.98
Lophotriccus pileatus	Scale-crested pygmy-tyrant	2	151	0.94	0.04	0.85	0.99	0.58	0.12	0.31	0.80
Todirostrum cinereum	Common tody-flycatcher	2	36	0.54	0.12	0.29	0.75	0.67	0.19	0.29	0.95
Tolmomyias sulphurescens	Yellow-olive flycatcher	3	131	0.84	0.07	0.70	0.96	0.66	0.10	0.44	0.82

Appendix B. (Continued)

Myiarchus tuberculifer	Dusky-capped flycatcher	2	84	0.81	0.06	0.67	0.92	0.58	0.10	0.37	0.76
Megarhynchus pitangua	Boat-billed flycatcher	3	100	0.88	0.07	0.73	0.99	0.70	0.09	0.48	0.85
Myiozetetes similis	Social flycatcher	3	47	0.66	0.19	0.26	0.97	0.80	0.07	0.64	0.93
Tyrannus melancholicus	Tropical kingbird	3	42	0.64	0.23	0.16	0.97	0.73	0.08	0.54	0.87
Pachyramphus polychopterus	White-winged becard	2	62	0.70	0.10	0.47	0.87	0.73	0.09	0.54	0.90
Corapipo altera	White-ruffed manakin	2	158	0.91	0.04	0.81	0.98	0.50	0.11	0.27	0.71
Pipra coronata	Blue-crowned manakin	1	58	0.66	0.12	0.42	0.87	0.48	0.14	0.17	0.73
Hylophilus decurtatus	Lesser greenlet	2	172	0.93	0.03	0.86	0.98	0.55	0.12	0.32	0.76
Vireolanius pulchellus	Green shrike-vireo	2	41	0.57	0.09	0.39	0.74	0.44	0.19	0.09	0.81
Thryothorus rutilus	Rufous-breasted wren	3	203	0.93	0.03	0.86	0.98	0.71	0.08	0.54	0.85
Thryothorus modestus	Plain wren	3	42	0.62	0.25	0.08	0.98	0.74	0.07	0.59	0.86
Troglodytes aedon	House wren	3	79	0.66	0.25	0.07	0.98	0.81	0.06	0.68	0.91
Henicorhina leucosticta	White-breasted wood-wren	1	201	0.97	0.02	0.93	1.00	0.55	0.10	0.34	0.75
Polioptila plumbea	Tropical gnatcatcher	2	75	0.85	0.08	0.65	0.96	0.73	0.14	0.42	0.94
Catharus aurantiirostris	Orange-billed nightingale-thrush	2	141	0.76	0.07	0.62	0.88	0.81	0.06	0.67	0.91
Turdus grayi	Clay-colored thrush	3	114	0.77	0.08	0.60	0.90	0.79	0.08	0.63	0.93
Turdus assimilis	White-throated thrush	1	75	0.94	0.05	0.80	1.00	0.49	0.12	0.23	0.71
Parula pitiayumi	Tropical parula	2	104	0.90	0.04	0.80	0.97	0.49	0.14	0.21	0.74
Myioborus miniatus	Slate-throated redstart	2	79	0.72	0.10	0.50	0.89	0.54	0.13	0.27	0.77
Basileuterus culicivorus	Golden-crowned warbler	2	49	0.73	0.07	0.59	0.85	0.56	0.11	0.32	0.77
Basileuterus rufifrons	Rufous-capped warbler	2	42	0.67	0.14	0.37	0.91	0.74	0.10	0.51	0.90
Coereba flaveola	Bananaquit	2	62	0.72	0.12	0.43	0.91	0.79	0.07	0.64	0.92
Chlorospingus ophthalmicus	Common bush-tanager	2	61	0.65	0.08	0.49	0.80	0.35	0.14	0.09	0.62
Habia rubica	Red-crowned ant-tanager	1	39	0.66	0.11	0.43	0.88	0.49	0.12	0.25	0.72
Ramphocelus costaricensis	Cherrie's tanager	3	49	0.51	0.28	0.03	0.95	0.80	0.06	0.68	0.91
Thraupis episcopus	Blue-gray tanager	3	133	0.64	0.12	0.38	0.85	0.82	0.06	0.69	0.93
Tangara larvata	Golden-hooded tanager	3	164	0.90	0.06	0.77	0.99	0.81	0.06	0.68	0.92
Tangara guttata	Speckled tanager	1	56	0.93	0.04	0.82	0.99	0.43	0.19	0.08	0.77
Tangara gyrola	Bay-headed tanager	2	59	0.81	0.10	0.58	0.95	0.69	0.15	0.35	0.92
Tangara icterocephala	Silver-throated tanager	2	169	0.89	0.04	0.79	0.97	0.72	0.16	0.42	0.98
Chlorophanes spiza	Green honeycreeper	2	44	0.64	0.16	0.32	0.91	0.59	0.20	0.15	0.91
Sporophila americana	Variable seedeater	3	40	0.62	0.26	0.06	0.97	0.73	0.08	0.55	0.87
Tiaris olivaceus	Yellow-faced grassquit	3	39	0.62	0.26	0.05	0.98	0.74	0.08	0.56	0.88
Arremon aurantiirostris	Orange-billed sparrow	1	149	0.96	0.02	0.90	0.99	0.60	0.12	0.34	0.81
Buarremon brunneinucha	Chestnut-capped brush-finch	1	34	0.56	0.11	0.34	0.75	0.37	0.20	0.03	0.72

Appendix B. (Continued)

Saltator striatipectus	Streaked saltator	3	62	0.71	0.16	0.38	0.96	0.76	0.08	0.59	0.91
Saltator maximus	Buff-throated saltator	3	156	0.91	0.05	0.80	0.98	0.79	0.06	0.66	0.90
Psarocolius decumanus	Crested oropendola	3	32	0.46	0.15	0.17	0.72	0.59	0.13	0.29	0.79
Euphonia luteicapilla	Yellow-crowned euphonia	2	42	0.60	0.11	0.35	0.79	0.67	0.17	0.25	0.93
Euphonia imitans	Spot-crowned euphonia	2	60	0.77	0.11	0.54	0.94	0.54	0.19	0.14	0.86
Carduelis psaltria	Lesser goldfinch	3	42	0.62	0.27	0.05	0.97	0.74	0.07	0.58	0.86

APPENDIX C

Appendix C. Mean, standard deviation (SD), and 95% posterior intervals for species-specific probabilities of colonization of forest and non-forest, as estimated using the hierarchical community model.

		Colonization Forest				Colonization Non-forest			
Scientific name	Common name	*Mean*	*SD*	*95% posterior interval*		*Mean*	*SD*	*95% posterior interval*	
Crypturellus soui	Little tinamou	0.53	0.20	0.20	0.97	0.08	0.07	0.001800	0.234154
Patagioenas speciosa	Scaled pigeon	0.59	0.20	0.22	0.95	0.05	0.10	0.000016	0.259033
Patagioenas nigrirostris	Short-billed pigeon	0.15	0.11	0.01	0.40	0.04	0.11	0.000009	0.318798
Leptotila verreauxi	White-tipped dove	0.47	0.26	0.05	0.97	0.21	0.25	0.000070	0.871804
Geotrygon chiriquensis	Chiriqui quail-dove	0.25	0.16	0.04	0.67	0.04	0.05	0.001375	0.129544
Aratinga finschi	Crimson-fronted parakeet	0.48	0.20	0.14	0.95	0.24	0.18	0.010021	0.702890
Piaya cayana	Squirrel cuckoo	0.35	0.26	0.01	0.92	0.16	0.23	0.000064	0.923508
Phaethornis guy	Green hermit	0.71	0.21	0.23	0.99	0.14	0.17	0.000220	0.656582
Phaethornis striigularis	Stripe-throated hermit	0.81	0.13	0.50	0.98	0.04	0.09	0.000013	0.264055
Campylopterus hemileucurus	Violet sabrewing	0.05	0.04	0.00	0.14	0.05	0.13	0.000010	0.425191
Amazilia decora	Charming hummingbird	0.26	0.13	0.04	0.55	0.04	0.11	0.000019	0.306465
Amazilia tzacatl	Rufous-tailed hummingbird	0.26	0.11	0.10	0.51	0.48	0.21	0.111056	0.886250
Trogon violaceus	Violaceous trogon	0.56	0.26	0.03	0.96	0.02	0.05	0.000016	0.134820
Momotus momota	Blue-crowned motmot	0.89	0.11	0.59	1.00	0.04	0.07	0.000016	0.208829
Ramphastos swainsonii	Chestnut-mandibled toucan	0.18	0.08	0.05	0.36	0.04	0.05	0.000951	0.153034
Picumnus olivaceus	Olivaceous piculet	0.63	0.25	0.06	0.98	0.24	0.28	0.000337	0.962421
Melanerpes rubricapillus	Red-crowned woodpecker	0.25	0.19	0.01	0.71	0.45	0.35	0.000839	0.977925
Automolus ochrolaemus	Buff-throated foliage-gleaner	0.40	0.31	0.01	0.97	0.03	0.05	0.000014	0.165481
Automolus rubiginosus	Ruddy foliage-gleaner	0.13	0.07	0.02	0.26	0.04	0.09	0.000551	0.170795
Sittasomus griseicapillus	Olivaceous woodcreeper	0.68	0.25	0.07	0.99	0.03	0.08	0.000014	0.190002
Xiphorhynchus erythropygius	Spotted woodcreeper	0.17	0.09	0.02	0.37	0.03	0.07	0.000599	0.134238
Lepidocolaptes souleyetii	Streak-headed woodcreeper	0.32	0.25	0.01	0.87	0.14	0.10	0.004735	0.384167
Thamnophilus bridgesi	Black-hooded antshrike	0.29	0.19	0.01	0.74	0.04	0.11	0.000016	0.354298
Dysithamnus mentalis	Plain antvireo	0.21	0.12	0.04	0.51	0.03	0.04	0.000733	0.123251
Formicarius analis	Black-faced antthrush	0.16	0.06	0.04	0.29	0.03	0.04	0.000353	0.116706
Myiopagis viridicata	Greenish elaenia	0.11	0.07	0.01	0.28	0.04	0.06	0.000019	0.205707
Elaenia flavogaster	Yellow-bellied elaenia	0.33	0.27	0.01	0.95	0.20	0.13	0.012717	0.499720
Mionectes oleagineus	Ochre-bellied flycatcher	0.45	0.12	0.24	0.73	0.10	0.19	0.000048	0.794946
Zimmerius vilissimus	Paltry tyrannulet	0.76	0.20	0.20	0.99	0.33	0.35	0.000208	0.990088
Lophotriccus pileatus	Scale-crested pygmy-tyrant	0.75	0.26	0.07	1.00	0.03	0.03	0.000018	0.117016
Todirostrum cinereum	Common tody-flycatcher	0.06	0.05	0.00	0.18	0.33	0.30	0.000244	0.960113

Appendix C. (Continued)

Tolmomyias sulphurescens	Yellow-olive flycatcher	0.61	0.20	0.17	0.93	0.06	0.05	0.001255	0.200047
Myiarchus tuberculifer	Dusky-capped flycatcher	0.40	0.17	0.12	0.81	0.01	0.02	0.000011	0.066920
Megarhynchus pitangua	Boat-billed flycatcher	0.67	0.22	0.20	0.99	0.10	0.08	0.003755	0.287430
Myiozetetes similis	Social flycatcher	0.26	0.22	0.01	0.84	0.41	0.25	0.026109	0.925807
Tyrannus melancholicus	Tropical kingbird	0.33	0.24	0.02	0.93	0.12	0.09	0.003811	0.344862
Pachyramphus polychopterus	White-winged becard	0.15	0.10	0.01	0.38	0.03	0.07	0.000016	0.215008
Corapipo altera	White-ruffed manakin	0.80	0.18	0.28	0.99	0.01	0.02	0.000012	0.070241
Pipra coronata	Blue-crowned manakin	0.19	0.08	0.04	0.35	0.03	0.04	0.000430	0.092877
Hylophilus decurtatus	Lesser greenlet	0.81	0.16	0.37	0.99	0.04	0.04	0.000939	0.136226
Vireolanius pulchellus	Green shrike-vireo	0.12	0.05	0.04	0.24	0.04	0.09	0.000015	0.273031
Thryothorus rutilus	Rufous-breasted wren	0.45	0.19	0.12	0.83	0.11	0.08	0.003666	0.293281
Thryothorus modestus	Plain wren	0.33	0.26	0.01	0.92	0.16	0.10	0.016191	0.399680
Troglodytes aedon	House wren	0.36	0.26	0.01	0.95	0.14	0.09	0.016367	0.375686
Henicorhina leucosticta	White-breasted wood-wren	0.24	0.17	0.04	0.75	0.02	0.02	0.000437	0.076280
Polioptila plumbea	Tropical gnatcatcher	0.31	0.22	0.01	0.84	0.19	0.21	0.000238	0.806121
Catharus aurantiirostris	Orange-billed nightingale-thrush	0.35	0.11	0.16	0.57	0.02	0.03	0.000012	0.117845
Turdus grayi	Clay-colored thrush	0.25	0.12	0.05	0.50	0.52	0.23	0.101835	0.943481
Turdus assimilis	White-throated thrush	0.26	0.17	0.05	0.71	0.03	0.03	0.000337	0.089562
Parula pitiayumi	Tropical parula	0.53	0.20	0.13	0.86	0.02	0.03	0.000014	0.101015
Myioborus miniatus	Slate-throated redstart	0.35	0.13	0.11	0.62	0.03	0.04	0.000025	0.136815
Basileuterus culicivorus	Golden-crowned warbler	0.06	0.05	0.00	0.18	0.02	0.02	0.000007	0.077558
Basileuterus rufifrons	Rufous-capped warbler	0.19	0.17	0.01	0.71	0.07	0.10	0.000028	0.370051
Coereba flaveola	Bananaquit	0.31	0.24	0.01	0.92	0.03	0.06	0.000015	0.202781
Chlorospingus ophthalmicus	Common bush-tanager	0.03	0.03	0.00	0.12	0.01	0.01	0.000011	0.050259
Habia rubica	Red-crowned ant-tanager	0.22	0.09	0.08	0.42	0.02	0.02	0.000399	0.082792
Ramphocelus costaricensis	Cherrie's tanager	0.40	0.24	0.06	0.93	0.12	0.11	0.001751	0.420530
Thraupis episcopus	Blue-gray tanager	0.18	0.10	0.01	0.40	0.22	0.18	0.005384	0.660472
Tangara larvata	Golden-hooded tanager	0.70	0.23	0.15	0.99	0.16	0.14	0.002419	0.527497
Tangara guttata	Speckled tanager	0.18	0.12	0.02	0.52	0.05	0.08	0.001109	0.211151
Tangara gyrola	Bay-headed tanager	0.38	0.24	0.01	0.89	0.11	0.19	0.000041	0.797057
Tangara icterocephala	Silver-throated tanager	0.74	0.15	0.39	0.96	0.58	0.32	0.006888	0.988502
Chlorophanes spiza	Green honeycreeper	0.50	0.21	0.10	0.92	0.12	0.21	0.000044	0.866690
Sporophila americana	Variable seedeater	0.35	0.27	0.01	0.94	0.26	0.14	0.049737	0.574100
Tiaris olivaceus	Yellow-faced grassquit	0.35	0.27	0.01	0.94	0.18	0.10	0.017533	0.416222
Arremon aurantiirostris	Orange-billed sparrow	0.28	0.17	0.07	0.71	0.04	0.04	0.000875	0.168541

Appendix C. (Continued)

Buarremon brunneinucha	Chestnut-capped brush-finch	0.12	0.05	0.03	0.23	0.03	0.04	0.000524	0.110465
Saltator striatipectus	Streaked saltator	0.27	0.20	0.02	0.80	0.53	0.25	0.092457	0.973661
Saltator maximus	Buff-throated saltator	0.26	0.16	0.01	0.62	0.12	0.11	0.001876	0.391932
Psarocolius decumanus	Crested oropendola	0.11	0.06	0.02	0.26	0.04	0.05	0.000665	0.180051
Euphonia luteicapilla	Yellow-crowned euphonia	0.07	0.06	0.00	0.21	0.20	0.27	0.000105	0.952075
Euphonia imitans	Spot-crowned euphonia	0.60	0.20	0.09	0.91	0.06	0.13	0.000011	0.457726
Carduelis psaltria	Lesser goldfinch	0.34	0.27	0.01	0.94	0.17	0.10	0.018762	0.410330

APPENDIX D

Appendix D. Mean, standard deviation (SD), and 95% posterior intervals for species-specific probabilities of detection of forest and non-forest, as estimated using the hierarchical community model.

Scientific name	Common name	Detection Forest				Detection Non-forest			
		Mean	*SD*	*95% posterior interval*		*Mean*	*SD*	*95% posterior interval*	
Crypturellus soui	Little tinamou	0.33	0.06	0.21	0.46	0.46	0.08	0.31	0.62
Patagioenas speciosa	Scaled pigeon	0.33	0.06	0.22	0.45	0.27	0.10	0.10	0.50
Patagioenas nigrirostris	Short-billed pigeon	0.36	0.06	0.25	0.49	0.16	0.16	0.01	0.63
Leptotila verreauxi	White-tipped dove	0.21	0.08	0.09	0.41	0.36	0.07	0.24	0.51
Geotrygon chiriquensis	Chiriqui quail-dove	0.17	0.05	0.10	0.28	0.32	0.21	0.03	0.80
Aratinga finschi	Crimson-fronted parakeet	0.19	0.07	0.09	0.34	0.38	0.07	0.25	0.51
Piaya cayana	Squirrel cuckoo	0.30	0.04	0.22	0.39	0.10	0.06	0.02	0.26
Phaethornis guy	Green hermit	0.51	0.04	0.42	0.59	0.20	0.09	0.07	0.41
Phaethornis striigularis	Stripe-throated hermit	0.29	0.05	0.20	0.39	0.17	0.10	0.04	0.41
Campylopterus hemileucurus	Violet sabrewing	0.51	0.08	0.36	0.66	0.14	0.14	0.01	0.55
Amazilia decora	Charming hummingbird	0.41	0.06	0.30	0.54	0.16	0.16	0.01	0.57
Amazilia tzacatl	Rufous-tailed hummingbird	0.33	0.09	0.16	0.51	0.53	0.06	0.41	0.64
Trogon violaceus	Violaceous trogon	0.20	0.05	0.13	0.32	0.23	0.11	0.07	0.48
Momotus momota	Blue-crowned motmot	0.39	0.05	0.30	0.48	0.28	0.09	0.13	0.48
Ramphastos swainsonii	Chestnut-mandibled toucan	0.37	0.06	0.27	0.49	0.18	0.16	0.01	0.58
Picumnus olivaceus	Olivaceous piculet	0.16	0.04	0.10	0.25	0.09	0.07	0.02	0.28
Melanerpes rubricapillus	Red-crowned woodpecker	0.35	0.05	0.27	0.45	0.32	0.06	0.21	0.46
Automolus ochrolaemus	Buff-throated foliage-gleaner	0.26	0.04	0.19	0.34	0.24	0.10	0.08	0.46
Automolus rubiginosus	Ruddy foliage-gleaner	0.36	0.08	0.22	0.53	0.17	0.16	0.01	0.55
Sittasomus griseicapillus	Olivaceous woodcreeper	0.17	0.04	0.10	0.25	0.22	0.11	0.06	0.47
Xiphorhynchus erythropygius	Spotted woodcreeper	0.29	0.05	0.20	0.39	0.16	0.18	0.00	0.62
Lepidocolaptes souleyetii	Streak-headed woodcreeper	0.39	0.04	0.31	0.48	0.49	0.11	0.27	0.69
Thamnophilus bridgesi	Black-hooded antshrike	0.24	0.06	0.15	0.37	0.13	0.14	0.01	0.53
Dysithamnus mentalis	Plain antvireo	0.37	0.05	0.28	0.47	0.40	0.13	0.18	0.68
Formicarius analis	Black-faced antthrush	0.61	0.07	0.47	0.73	0.18	0.19	0.00	0.66
Myiopagis viridicata	Greenish elaenia	0.34	0.06	0.23	0.47	0.32	0.10	0.15	0.55
Elaenia flavogaster	Yellow-bellied elaenia	0.02	0.03	0.00	0.06	0.43	0.07	0.31	0.57
Mionectes oleagineus	Ochre-bellied flycatcher	0.41	0.06	0.28	0.54	0.12	0.09	0.02	0.35
Zimmerius vilissimus	Paltry tyrannulet	0.59	0.04	0.51	0.67	0.22	0.05	0.14	0.31
Lophotriccus pileatus	Scale-crested pygmy-tyrant	0.58	0.03	0.51	0.65	0.35	0.11	0.15	0.59
Todirostrum cinereum	Common tody-flycatcher	0.36	0.09	0.20	0.55	0.24	0.07	0.13	0.40

Appendix D. (Continued)

Tolmomyias sulphurescens	Yellow-olive flycatcher	0.60	0.05	0.51	0.69	0.42	0.11	0.22	0.62
Myiarchus tuberculifer	Dusky-capped flycatcher	0.43	0.05	0.34	0.52	0.52	0.12	0.28	0.74
Megarhynchus pitangua	Boat-billed flycatcher	0.36	0.04	0.29	0.45	0.40	0.08	0.26	0.57
Myiozetetes similis	Social flycatcher	0.10	0.07	0.03	0.29	0.36	0.06	0.25	0.49
Tyrannus melancholicus	Tropical kingbird	0.09	0.06	0.03	0.25	0.41	0.07	0.29	0.55
Pachyramphus polychopterus	White-winged becard	0.38	0.06	0.27	0.50	0.28	0.07	0.15	0.43
Corapipo altera	White-ruffed manakin	0.63	0.04	0.56	0.70	0.61	0.14	0.32	0.87
Pipra coronata	Blue-crowned manakin	0.48	0.07	0.35	0.62	0.23	0.13	0.04	0.55
Hylophilus decurtatus	Lesser greenlet	0.70	0.03	0.64	0.76	0.50	0.13	0.25	0.74
Vireolanius pulchellus	Green shrike-vireo	0.60	0.07	0.45	0.74	0.16	0.16	0.01	0.59
Thryothorus rutilus	Rufous-breasted wren	0.76	0.03	0.69	0.82	0.62	0.08	0.47	0.76
Thryothorus modestus	Plain wren	0.01	0.03	0.00	0.05	0.59	0.07	0.47	0.72
Troglodytes aedon	House wren	0.01	0.01	0.00	0.03	0.75	0.05	0.66	0.84
Henicorhina leucosticta	White-breasted wood-wren	0.79	0.03	0.73	0.84	0.69	0.12	0.44	0.89
Polioptila plumbea	Tropical gnatcatcher	0.32	0.05	0.24	0.42	0.23	0.08	0.11	0.42
Catharus aurantiirostris	Orange-billed nightingale-thrush	0.57	0.05	0.47	0.66	0.72	0.06	0.61	0.82
Turdus grayi	Clay-colored thrush	0.45	0.05	0.35	0.55	0.36	0.06	0.25	0.47
Turdus assimilis	White-throated thrush	0.34	0.04	0.26	0.42	0.32	0.13	0.11	0.59
Parula pitiayumi	Tropical parula	0.55	0.04	0.47	0.63	0.38	0.15	0.13	0.70
Myioborus miniatus	Slate-throated redstart	0.48	0.05	0.38	0.58	0.39	0.12	0.18	0.65
Basileuterus culicivorus	Golden-crowned warbler	0.52	0.06	0.39	0.63	0.43	0.12	0.20	0.68
Basileuterus rufifrons	Rufous-capped warbler	0.17	0.06	0.08	0.31	0.42	0.08	0.27	0.59
Coereba flaveola	Bananaquit	0.25	0.06	0.15	0.37	0.38	0.07	0.26	0.52
Chlorospingus ophthalmicus	Common bush-tanager	0.60	0.06	0.49	0.71	0.70	0.12	0.44	0.90
Habia rubica	Red-crowned ant-tanager	0.36	0.07	0.23	0.51	0.38	0.12	0.16	0.63
Ramphocelus costaricensis	Cherrie's tanager	0.11	0.08	0.03	0.32	0.46	0.06	0.34	0.58
Thraupis episcopus	Blue-gray tanager	0.42	0.06	0.31	0.55	0.63	0.05	0.53	0.73
Tangara larvata	Golden-hooded tanager	0.53	0.04	0.45	0.61	0.48	0.06	0.37	0.59
Tangara guttata	Speckled tanager	0.27	0.04	0.20	0.34	0.28	0.17	0.05	0.66
Tangara gyrola	Bay-headed tanager	0.30	0.05	0.22	0.42	0.13	0.07	0.04	0.32
Tangara icterocephala	Silver-throated tanager	0.59	0.04	0.51	0.66	0.33	0.07	0.21	0.47
Chlorophanes spiza	Green honeycreeper	0.29	0.06	0.19	0.42	0.09	0.07	0.02	0.28
Sporophila americana	Variable seedeater	0.01	0.04	0.00	0.04	0.50	0.06	0.37	0.62
Tiaris olivaceus	Yellow-faced grassquit	0.01	0.04	0.00	0.04	0.50	0.06	0.38	0.63
Arremon aurantiirostris	Orange-billed sparrow	0.59	0.04	0.51	0.66	0.46	0.10	0.27	0.67

Appendix D. (Continued)

Buarremon brunneinucha	Chestnut-capped brush-finch	0.46	0.07	0.32	0.61	0.15	0.18	0.00	0.59
Saltator striatipectus	Streaked saltator	0.14	0.07	0.05	0.30	0.48	0.06	0.37	0.60
Saltator maximus	Buff-throated saltator	0.53	0.04	0.45	0.62	0.47	0.06	0.36	0.59
Psarocolius decumanus	Crested oropendola	0.39	0.08	0.25	0.55	0.36	0.12	0.12	0.60
Euphonia luteicapilla	Yellow-crowned euphonia	0.32	0.06	0.21	0.44	0.14	0.05	0.06	0.27
Euphonia imitans	Spot-crowned euphonia	0.37	0.05	0.27	0.48	0.12	0.10	0.01	0.40
Carduelis psaltria	Lesser goldfinch	0.01	0.03	0.00	0.05	0.59	0.07	0.46	0.72

APPENDIX E

APPENDIX E. List of species of conservation concern, their forest dependency (FD) category the mean and 95% posterior interval for species-specific probabilities of occupancy of forest and non-forest, and colonization of non-forest, as estimated using the hierarchical community model. Species were defined by having mean forest occupancy estimates greater than 0.6, occupancy in non-forest less or equal to 0.6, and colonization of non-forest less than 0.2.

			Occupancy Forest			Occupancy Non- forest			Colonization Non- forest		
Scientific name	Common name	FD	*Mean*	*95% posterior interval*		*Mean*	*95% posterior interval*		*Mean*	*95% posterior interval*	
Patagioenas nigrirostris	Short-billed pigeon	MED	0.75	0.53	0.90	0.44	0.09	0.80	0.0397	0.0000	0.3188
Geotrygon chiriquensis	Chiriqui quail-dove	HIGH	0.85	0.50	0.99	0.36	0.03	0.70	0.0361	0.0014	0.1295
Piaya cayana	Squirrel cuckoo	MED	0.83	0.58	0.96	0.60	0.16	0.90	0.1564	0.0001	0.9235
Amazilia decora	Charming hummingbird	MED	0.74	0.56	0.89	0.44	0.10	0.80	0.0394	0.0000	0.3065
Trogon violaceus	Violaceous trogon	MED	0.74	0.40	0.96	0.59	0.33	0.81	0.0228	0.0000	0.1348
Ramphastos swainsonii	Chestnut-mandibled toucan	HIGH	0.82	0.67	0.94	0.40	0.03	0.74	0.0388	0.0010	0.1530
Automolus rubiginosus	Ruddy foliage-gleaner	HIGH	0.62	0.34	0.85	0.42	0.03	0.78	0.0402	0.0006	0.1708
Sittasomus griseicapillus	Olivaceous woodcreeper	MED	0.76	0.43	0.97	0.58	0.30	0.82	0.0297	0.0000	0.1900
Xiphorhynchus erythropygius	Spotted woodcreeper	HIGH	0.84	0.66	0.95	0.37	0.02	0.73	0.0322	0.0006	0.1342
Thamnophilus bridgesi	Black-hooded antshrike	MED	0.62	0.26	0.90	0.45	0.09	0.84	0.0424	0.0000	0.3543
Dysithamnus mentalis	Plain antvireo	HIGH	0.86	0.72	0.96	0.51	0.22	0.76	0.0341	0.0007	0.1233
Formicarius analis	Black-faced antthrush	HIGH	0.71	0.52	0.86	0.38	0.03	0.73	0.0293	0.0004	0.1167
Lophotriccus pileatus	Scale-crested pygmy-tyrant	MED	0.94	0.85	0.99	0.58	0.31	0.80	0.0252	0.0000	0.1170
Myiarchus tuberculifer	Dusky-capped flycatcher	MED	0.81	0.67	0.92	0.58	0.37	0.76	0.0140	0.0000	0.0669
Corapipo altera	White-ruffed manakin	MED	0.91	0.81	0.98	0.50	0.27	0.71	0.0137	0.0000	0.0702
Pipra coronata	Blue-crowned manakin	HIGH	0.66	0.42	0.87	0.48	0.17	0.73	0.0272	0.0004	0.0929
Hylophilus decurtatus	Lesser greenlet	MED	0.93	0.86	0.98	0.55	0.32	0.76	0.0365	0.0009	0.1362
Henicorhina leucosticta	White-breasted wood-wren	HIGH	0.97	0.93	1.00	0.55	0.34	0.75	0.0229	0.0004	0.0763
Turdus assimilis	White-throated thrush	HIGH	0.94	0.80	1.00	0.49	0.23	0.71	0.0251	0.0003	0.0896
Parula pitiayumi	Tropical parula	MED	0.90	0.80	0.97	0.49	0.21	0.74	0.0195	0.0000	0.1010
Myioborus miniatus	Slate-throated redstart	MED	0.72	0.50	0.89	0.54	0.27	0.77	0.0298	0.0000	0.1368
Basileuterus culicivorus	Golden-crowned warbler	MED	0.73	0.59	0.85	0.56	0.32	0.77	0.0152	0.0000	0.0776
Chlorospingus ophthalmicus	Common bush-tanager	MED	0.65	0.49	0.80	0.35	0.09	0.62	0.0105	0.0000	0.0503
Habia rubica	Red-crowned ant-tanager	HIGH	0.66	0.43	0.88	0.49	0.25	0.72	0.0242	0.0004	0.0828
Tangara guttata	Speckled tanager	HIGH	0.93	0.82	0.99	0.43	0.08	0.77	0.0480	0.0011	0.2112
Chlorophanes spiza	Green honeycreeper	MED	0.64	0.32	0.91	0.59	0.15	0.91	0.1220	0.0000	0.8667
Euphonia imitans	Spot-crowned euphonia	MED	0.77	0.54	0.94	0.54	0.14	0.86	0.0610	0.0000	0.4577